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SOIL-FERTILITY STANDARDS FOR GAME FOOD PLANTS[1]

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Surveys of forest soils and vegetation in Wisconsin have indicated that many important fruit-bearing trees and shrubs have greatly restricted quantitative distribution. Mountain ash, wild crab apple, highbush cranberry, nannyberry, thorn apple, and wild plum are examples. These may not comprise any large part of the total food of game animals, but by reason of their content of vitamins and other functional substances they may be essential in wildlife welfare.

In the spring of 1944, a detailed study was started of the soil requirements of a few species for use in future artificial propagation. The problem included the establishment of levels of soil fertility required by different species for proper development in the nursery, and determination of the range of soil conditions suitable for these species in the field. As a by-product, information was obtained on the value of various soil-forest types in producing game food.

It has been suggested that "The crying need at this stage of the conservation movement is *specific definition* of the environment needed by each species" (Leopold, 1936). The present paper attempts to express some environmental conditions in terms of concrete data.

SPECIES FOR ARTIFICIAL PROPAGATION

Only a few of the more desirable woody plants capable of nursery propagation were studied: red cedar (*Juniperus virginiana*), mountain ash (*Sorbus americana*), wild crabapple (*Malus ioensis*), hawthorne (*Crategus punctata, C. succulenta*), black cherry (*Prunus serotina*), highbush cranberry (*Viburnum trilobum*), and red-osier dogwood (*Cornus stolonifera*). The choice of these species was made after considering several aspects, namely: direct value as game food; ability to maintain the fruit beyond the summer, and, especially in winter; value as game cover; present status of natural distribution; facility of artificial propagation; and general silvicultural desirability.

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A number of other species (nannyberry, dockmackie, black haw, wild plum, gray dogwood, bittersweet, and wild grape) were investigated, but wartime limitations prevented accumulation of statistically significant data. Any future enlargement of the program must be made with reservation, since use of many species complicates both nursery operation and planting procedure.

SOIL FERTILITY IN NURSERIES

In early soil investigations, the only way to study the effects of plant nutrients and associated fertility factors was by empirical trials in the greenhouse and on sample plots. This proved of little value in dealing with the many and mutually interrelated variables of nursery soil fertility. In addition to the involved experimental procedure, the "optimum" growth, as measured on the basis of dry matter produced, proved of doubtful importance in raising seedlings for reforestation. Stock having the maximum dry weight is too expensive to raise, and often is too difficult to plant. Unreasonably large and abnormally "forced" seedlings often show decreased vigor and poor survival when put out on exposed cutover lands.

The recent progress in analytical determinations of soil reaction, exchange properties, and available nutrients, however, enabled use of a more fruitful approach—the analysis of soils under productive stands of various species. The statistical data from analyses of such natural seedbeds give a close approach to the physiological optimum of growth conditions. Such data indicate not only the amount of nutrients, which may be variable, but the constant ratio of various constituents, an important prerequisite to balanced nutrition of seedlings. Experience in nurseries and greenhouses has shown that the natural fertility levels help to prevent starvation of nursery stock and also unreasonably rapid growth or abnormal development.

Soil samples accordingly were collected throughout Wisconsin from areas supporting vigorous and bearing trees and shrubs of the desired species. There was a general tendency to confine sampling largely to soils of coarser texture, low in organic matter, and having critical pH values. For most species, between 40 and 60 samples were collected and analyzed to assure statistically significant results. The methods for collecting soil samples, laboratory analysis, and treatment of data have already been described (Wilde, 1938; Wilde and Patzer, 1940).

Results of the analyses are given in Table 1. The approximate levels or ranges of soil fertility factors (in round numbers) that may serve as standards for raising different game food species in nurseries are shown in Table 2. Directions for the adjustment of fertility in nursery soils are given in the literature quoted.

SUITABLE FIELD SOILS

The mere occurrence of a species on a certain site is not necessarily proof of its ability to produce an abundant food crop. Many game food trees and shrubs in Wisconsin do not always have satisfactory production of seeds and fruits. Their restricted bearing appears due to the low soil fertility as well as to

TABLE 1.—CHARACTERISTICS OF WISCONSIN SOILS SUPPORTING SOME GAME FOOD PLANTS.

Species	Reaction, pH	Base exchange capacity M.E./ 100 g.	Total nitrogen, percentage	Pounds per acre available			Replaceable calcium M.E./ 100 g.
				Nitrogen	P_2O_5	K_2O	
Red cedar (*Juniperus virginiana*)	6.7±.12	2.27±.2	.041±.01	10.2	27.3±4.7	57.1±12.1	1.7±.2
Mountain ash (*Sorbus americana*)	4.9±.09	5.01±.2	.061±.01	12.7	61.1±7.3	122.5±7.8	1.2±.1
Wild crabapple (*Malus ioensis*)	6.28±.09	5.83±.4	.068±.007	17.1	74.8±9.5	125.5±10.3	4.47±.5
Hawthorn (*Crategus punctata*)	5.36±.10	4.15±.3	.042±.006	12.1	57.5±6.6	126.3±9.2	1.7±.2
Black cherry (*Prunus serotina*)	5.35±.19	4.87±.3	.065±.004	12.7	52.6±5.4	115.5±8.0	1.9±.3
Red-osier dogwood (*Cornus stolonifera*)	5.35±.11	6.31±.3	.067±.007	14.3	78.3±12.0	158.3±14.4	2.9±.4
Highbush cranberry (*Viburnum trilobum*)	6.19±.18	6.41±.3	.099±.009	25.7	118.9±12.0	169.3±11.4	5.2±.4

deficiencies in light and to climatic extremes.

The present survey showed that Wisconsin has large areas of soils in a critical state of fertility so far as some game food plants are concerned, especially on burned-over podzols and coarse siliceous sands in which the destroyed organic matter had been the principal source of plant nutrients.

Hazel, one of the least exacting and widely distributed shrubs, is an example. In the autumn of 1944 there was an exceptionally abundant crop of hazel nuts in Wisconsin, but bushes on severely burned podzol areas in the north remained conspicuously barren. Bearberries (*Arctostaphylos uva-ursi*), which are widely distributed on sandy outwash in central Wisconsin, provide another striking example of meager fruit production on depleted soils. Observations by Leopold on red raspberry, sand cherry, and hazel growing on the poor sands of his farm in Sauk County, Wisconsin, show only vegetative propagation; there has been no fruit during the last ten years. The hazel and raspberry fruit regularly, however, on better soils of the same farm.

Even if a food crop is produced on soils deficient in some essential elements it may not have an adequate nutrient value for game. McLean *et al.* (1944) have shown that forage raised on soils of low fertility does not meet the requirements for normal development of farm animals. The observed deterioration of bones and other manifestations

TABLE 2.—STANDARDS OF SOIL FERTILITY FOR NURSERIES REARING GAME FOOD PLANTS.

Species	Reaction, *p*H	Base exchange capacity, M.E./100 g.	Total nitrogen percentage	Pounds per acre available			
				Nitrogen	P_2O_5	K_2O	Replaceable calcium
Red cedar	6.5–7.0	2.5	.04	10	30	75	800
Wild crabapple	6.0–6.5	6.0	.07	20	75	150	1700
Highbush cranberry	5.5–6.5	6.5	.10	25	120	175	2000
Red-osier dogwood	5.0–6.0	6.0	.07	15	75	150	1200
Black cherry	5.2–6.0	5.0	.07	15	75	125	800
Hawthorn	5.2–6.0	4.0	.05	10	60	125	600
Mountain ash	4.8–5.5	5.	.06	15	60	125	400

of malnutrition, in laboratory experiments, foretell the destiny of game confined to depleted soils. According to Albrecht (1943), the hunger of forest-inhabiting animals for bones testifies that the scant mineral supplies in such areas must be kept "rotating from one animal to another for their survival on the less fertile forest soils."

Artificial propagation of game food plants, like the problem of reforestation, carries implications not always obvious to a casual observer. In silviculture, the soil conditions should assure the survival of the planted tree species, and also a reasonably high rate of growth and the production of valuable wood. Similarly, in planting game food, there should be adequate soil fertility to maintain the species and enable production of a reasonably abundant food crop having sufficient nutrient value. Unless these requirements are fulfilled, the planting of game food cannot be regarded as satisfactory. The planting of each individual species therefore must be preceded by scrupulous selection of the site. Utmost benefit must be derived from the smaller areas of soil having slightly higher levels of fertility or more favorable site conditions.

Previous reforestation in Wisconsin indicates that the reaction of the soil, percentage of mineral colloids, content of organic matter, and the ground water table are the four soil factors with decisive influences on the growth of plantations. With tolerant species, success usually depends upon the presence of some nurse trees to provide partial shade and protection. Sites exposed to strong winds, hot southern or southwestern slopes, and frost pockets naturally are unfavorable for planting.

TABLE 3.—SITE REQUIREMENTS OF GAME FOOD PLANTS.

Species to be planted	Survival on exposed cut-over areas	Soil reaction pH	Minimum organic matter, percentage	Minimum percentage of silt and clay particles with ground water at depth of	
				1.5 to 2.5 ft.	2.5 or more ft.
Red cedar	Very high	5.7–8.0	0.5	none	none
Wild crabapple	High	5.5–8.0	1.2	12	30
Highbush cranberry	Fair	5.5–7.5	2.5	12	30
Red-osier dogwood	Fair	5.5–7.5	1.2	7	15
Black cherry	Fair	5.0–6.7	1.5	10	25
Mountain ash	High	4.7–6.0	1.7	7	15
Hawthorn	Very high	4.7–6.5	0.7	5	12

The influence of the soil reaction and texture and the humus content has received considerable attention in silviculture. The ground water level, however, has specific importance in the selection of sites for planting game food.

In planting trees for reforestation, a high water table usually results in retarded growth, production of timber with less desirable properties, high percentage of culls, and danger of windfall. These shortcomings are of little significance in planting game food. A high ground water level permits planting species having large water requirements on soils of coarse texture. The retarded decomposition of organic remains on sites influenced by the ground

water allows introduction of some exacting species on soils of less fertile mineral substrata. Skill in applying knowledge of ground water conditions is the key to success in the entire game food planting program.

Table 3 presents the site requirements for game food species thus far studied. These standards were arrived at by considering both the natural distribution of the species and their capacity of producing game food.

SILVICULTURAL ASPECTS OF PLANTING FOR GAME

Recent silvicultural literature has emphasized the biological and sociological importance of forests. Writers have emphasized the advantages of a well-balanced but diversified community of plants and animals in contrast to artificial and monogenic assemblages of trees alone. Such ideas, no matter how sound, until now remain mere abstractions. Practical silviculture still deals only with one component of the forest, trees, particularly those producing high yields of timber or pulpwood.

The practice of raising bigger and better trees at the least expense has been in effect throughout Central Europe for about two centuries, but the results leave much to be desired. In the long run the single-aged and single-species plantations did not have the ability to resist diseases and insect pests. The principal causes of vulnerability in the pure stands were assumed to be lack of natural biological control, restricted activity of symbiotic members, and partly arrested turnover of available nutrients.

One way to avoid the European experience (perhaps on a much greater scale) would be to build the forest with all its natural associates from the plant and animal kingdoms, and not merely as a barren framework of lumber. The introduction of some secondary trees and shrubs, particularly those providing sustenance for birds and other animals, may have a greater indirect silvicultural influence than a direct bearing on game management.

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LETHAL ALKALINITY FOR TROUT IN WATERS OF LOW SALT CONTENT

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In midsummer of 1942 a load of legal-sized rainbow trout was placed in Granite Basin Lake, of 10 acres, near Prescott, Arizona. Trout had been previously stocked in this water without incident, but within a few days this planting showed excessive mortality. No laboratory facilities were then employed by the Arizona Game Department, and a sample of the water was analyzed by a county agent. The analysis showed a pH of approximately 9.6, which was taken to be the causative factor in decimation of the trout.

In later years, other waters stocked for the first time with trout, or even those with a record of successful plantings, showed the same difficulty. No particular reason for the excessive alkalinity was deduced, other than that the condition resulted from runoff over limestone formations.

In 1944, the writer was employed by the Division of Fisheries of the Arizona Game Department to investigate this and other problems in the fisheries of the state. Ashurst Lake, near Flagstaff, of some 180 acres and an average depth of 10 feet, showed a serious mortality in rainbow trout stocked for the first time that spring, about three months previously. Preliminary scrutiny showed that approximately 2,000 trout had already died and others were succumbing gradually. The game ranger who first reported the condition stated that early symptoms involved complete loss of equilibrium and rapid whirling with the head protruding from the water as the fish apparently tried to emerge. Later this initial symptom subsided; when the writer visited the lake, the living but affected fish were swimming aimlessly near the surface. Most of these trout were blind in one or both eyes, which were whitened. The dead fish showed considerable fraying at the tip of the dorsal and caudal fins and slight deterioration at the edges of the gill membranes. All were in excellent physical condition, with abundant fat. Food conditions in the lake were phenomenal, about 80 per cent of the bottom area being covered with aquatic vegetation. In the shallower areas this was principally *Myriophyllum spicatum*, and deeper areas were covered with *Anacharis canadensis*, which reached almost to the surface.

The writer tested the water for various possible lethal factors. Carbon dioxide was not present, the oxygen measured 9.0 p.p.m., no ammonia was discovered, and there were no signs of other decomposition products. The pH, however, was over 10.2, the highest number on the comparator used, and this was taken to be the causative factor.

Ashurst Lake has neither inlet nor outlet; it is filled mainly by runoff from winter snows, but summer rains add slightly to the supply. Fluctuation in water level is about two feet from the spring high mark.

Chemical analysis of the water

showed the following concentrations of dissolved salts in parts per million:

Carbonates	46
Bicarbonates	54
Chlorides	7
Sulphates	trace
Calcium	25
Magnesium	7
Sodium	18
Total	157

The high pH was caused definitely by the carbonate concentration, which in the absence of any appreciable amount of buffering agents in water of low salt content, produces the basic reaction. This analysis is very similar to those of other high mountain waters both in total quantity of salts and in proportions.

It was suspected that the heavy growth of aquatic vegetation was the reason for the high carbonate content and the consequent high pH. Several months of investigation showed conclusively that the vegetation could be deemed the factor in raising the carbonate content through removal of carbon dioxide in the process of photosynthesis. Several items substantiated this conclusion. Stoneman Lake, of about 100 acres and 10 feet in depth, also had a pH of 10.2, and had a heavy growth of *Potamageton pectinatus* covering most of the bottom. A sudden and very heavy storm blew over that lake for a week in the summer of 1944, turning over the bottom and making the water quite turbid. A week after the storm it was still turbid, and the vegetation was cut off from any amount of light. A test then showed the pH to be 8.4, a great reduction.

All lakes and ponds of low salt content in this region that contain large amounts of vegetation were highly alkaline, but this condition disappears in winter when the vegetation is dormant; and the pH in all of these waters then drops to neutral or below. Some waters at lower elevations in Arizona that are filled with ground water or from long streams and which have heavy growths of vegetation showed pH reactions from neutral to 7.5. These waters were heavily buffered and had total contents of salt from 1,000 to 2,400 p.p.m.

While means were being developed to combat this problem in lakes, little thought was given to a similar possibility in streams. The year 1945 proved exceptional for the growth of algae and aquatic vegetation of all kinds, because of low waters in the spring and unusually long periods of cloudless days. The pH rose beyond what it had been in lakes checked at comparable times in 1944.

One July morning the Game Department planted about 1,200 legal-sized rainbow trout in the Little Colorado River near the town of Springerville. Nothing about this planting was different from many made earlier in this and other waters. About 2 P.M., the trout began dying by the hundreds, as reported a few days later by a sportsman of the district who had witnessed the planting and the later decimation. He charged that the death of the fish was caused by rough handling in planting, and that many of them had been dropped off a bridge into the water from a height of seven feet. Knowing that adult trout can stand even rougher treatment, such as being planted from airplanes, the writer looked for other causes.

One fact stood out—the eyes of the fish had turned white when they started

dying that afternoon. Alkalinity was immediately suspected, although it had never been found in lethal quantities in Arizona streams. A hasty trip to the stream and immediate check produced some puzzling results. The pH was only 7.3—far below any lethal concentration. Yet the dying fish showed all the characteristics associated with previous killings by alkali. Other streams of the district showed similar low pH readings; they all were fairly turbid from rains in the interval between the planting and the time of inspection.

Suspecting that the turbidity had been a factor in lowering the pH by cutting off sunlight from the stream vegetation, the writer waited until many had cleared, then checked them again, but the results still were baffling. The Little Colorado showed a pH of only 7.8 and other streams also were low except Black River, which at noon had a pH of 8.6. All streams still were slightly turbid. In the afternoon, after checking some lakes, the writer returned to Springerville and rechecked Buffalo Creek. When previously examined at 9 A.M. the pH was 7.6; now, at 3 P.M., six hours later, the pH was 8.6. The key to the whole situation was apparent, a rise of 1.0 in pH in five hours.

Immediately other streams were checked and the same result was observed. Although still murky, the Little Colorado at 6 P.M. had a pH of 8.4. When completely clear, as at the time of the fatalities, the pH undoubtedly was much higher. Unlike lakes, which retain a fairly constant pH during any 24-hour period, the streams, when clear, drop almost to neutral at night when photosynthesis is reversed, then build up through the day to a peak at about 5 P.M. A fork of Black River, which had a pH of 7.6 in the early morning, had risen to 9.4 by 5 P.M., easily enough to quickly kill fish fresh from neutral hatchery water; fish already in the water, however, were usually able to tolerate the changing condition. It is probable that water in the fish trucks reaches a fairly acid condition by the time the trucks reach the streams, especially on long hauls, although the matter needs to be checked with exactness. This contributes to the difficulty of hatchery fish becoming adjusted to the alkaline condition in streams. Tempering of the fish in this respect, an experiment yet to be tried, may prove beneficial.

Until the time of the above observations, four loads of trout planted in various streams had been almost completely decimated by high alkalinity. Thereafter, the hatchery men were instructed to plant only during or after a rain, when the streams would be turbid and neutral for a period of days in which the fish could be gradually acclimated to the rising alkalinity. As a result, no more trout were lost that year.

At the Pinetop State Hatchery, a flume 150 feet in length bypasses certain ponds. Normally this carries only a trickle of water through a heavy growth of *Spirogyra*. Hatchery water with a pH of 7.0 entering the head of this flume develops a pH of 7.3 by the time it traverses the 150 feet. Upon placing a small dab of mud from the neutral pond at the head of the flume, the water in the whole length became turbid, and the pH at the lower end

immediately dropped to 7.0, the same as at the flume entrance. It became evident that the photosynthesis of the algae was the cause of the base reaction; when sunlight was cut off by the turbidity, photosynthesis ceased.

Much remains to be learned of this phenomenon, one item being the relation of other factors that cause different pH levels to be lethal to the same fish. Some fish tolerated a pH as high as 10.2, as found in Ashurst Lake; many of them survived this condition, but when gill-netted the following spring (when the water was still neutral), a majority showed effects of the previous basic condition, with one or both eyes blinded, and frayed fins and gills. Some fish died in streams when the pH was as low as 8.8.

Another problem is the relative tolerance of different species and strains of trout to alkaline conditions. It may be possible through breeding to develop strains tolerant of base conditions or to change or control the water conditions so as to lower the pH during the summer by chemical or mechanical means. The writer has already developed one such successful method to be described elsewhere; because of the cost, however, it can be used only on small important waters. The cheapest and only practical method is to fit the fish to the water rather than the water to the fish, and this can be brought about only by breeding or discovering tolerant species desirable to the angler.

SUMMARY

Alkalinity has been found to be a highly lethal factor for trout in Arizona waters low in buffering agents. The symptoms are rapid spinning of the fish near the surface and attempts to leave the water, whitening of the eyes and complete blindness, fraying of the fins and gills with the frayed portions turning white, and death usually in a few hours. Any survivors usually later wander aimlessly around the shore line near the surface.

Alkaline conditions result from removal of carbon dioxide by aquatic vegetation in photosynthesis during daylight hours, resulting in the bicarbonates breaking down into carbonates.

Increasing the turbidity lowers the pH by cutting off light reaching the plants, with a consequent lowering of photosynthetic rate. Introducing fish in streams during periods of turbidity will permit them to gain tolerance for an alkaline condition by the time the pH again rises.

Trout were killed under certain conditions by a pH of 8.8, while some under other conditions survived a pH of 10.2.

This situation possibly may be overcome by changing the water conditions, by tempering the fish before planting, or by developing species or strains of fish tolerant to such high alkalinity.

SIGNIFICANCE OF RACIAL VARIATION IN BIRDS TO WILDLIFE MANAGEMENT

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Species

Even the most casual observer is aware of the fact that there are different kinds of birds about him. Some he recognizes by name. He may be able to distinguish the robin, blue jay, cardinal, English sparrow, or crow, as quite different from one another in appearance and habits, and in the sorts of places where they live and raise their young. The average observer would recognize them as species, distinguishable by their appearance, habits, voice, and habitats. What is more important, each bird recognizes its own kind. As a result one species does not ordinarily mate with the opposite sex of a different species; if it does, fertile offspring ordinarily do not result. This inability or disinclination of two kinds of birds to interbreed is the criterion usually accepted as distinguishing separate species.

Just as with human beings, probably no two individual birds of the same species look exactly alike. This is individual variation. Some individual variation among birds is great, as in the markedly different color phases of screech owls. One individual may be bright reddish brown and another reared in the same nest may be gray without a trace of reddishness. Red screech owls, however, recognize gray individuals as belonging to their own species and the two color phases interbreed freely. Many species of birds have rather distinct color phases, such as the red and gray phases of the ruffed grouse among game birds. In others the two sexes differ from one another more than many distinct species that live side by side without interbreeding. The brightly colored male of the ring-necked pheasant is quite unlike his brown and buff mate, yet the male and female pheasants have no difficulty in recognizing one another as of the same species. These differences, whether correlated with sex or distinct color phases independent of sex, are merely variations within the same species.

Races

Besides certain marked differences in sex and color phases, every bird is slightly different from every other because it derives from a different combination of hereditary characteristics. If a pair of birds with relatively similar hereditary features are kept apart from all others of their species they tend to produce offspring with relatively similar characters, and their offspring also tend to produce young with characters similar to the original pair. Poultry and livestock breeders are familiar with this principle, the development of "breeds" or "varieties." By selecting for breeding only individuals with certain desired characteristics they can develop strains of livestock in which most of the individuals have those characteristics.

In exactly the same way "nature" develops strains of birds particularly

suited to the environments in which they live. Nature is an exacting livestock breeder. There is a fine balance between ability and inability to survive the many dangers of a natural environment. Those individuals particularly well adapted have a greater chance than others to survive long enough to breed and pass on their hereditary characters to offspring. Thus geographic regions with a uniform set of environmental features develop relatively pure strains of animals preeminently suited to live in such environments. Furthermore, Twomey (1936: 122–132) has shown that certain migratory birds winter in areas with climatic conditions similar to those in which they breed.

If a bird species becomes so numerous in a region characterized by certain environmental conditions that the area will not support as many individuals as are produced, one of two things must happen to the excess population—it will be exterminated, or it will move to another region which has a different set of environmental conditions. Some obviously will attempt the latter.

Experience with transplanted species leads to the belief that in most cases of natural population spread the pioneers will not be sufficiently well adapted to the new environment to survive; here, however, the inherent nature of all species to vary enters importantly. After many unsuccessful invasions a few individuals may chance to have a combination of hereditary characteristics that will enable them to become established in the new environment and give rise to a new population. In successive generations the offspring better suited to the environment would be selected by nature for survival and perpetuate the species by passing on favorable characteristics to their progeny; individuals less well adapted to the environment would perish. The newly invaded area thus would eventually be populated by a variety differing slightly but significantly from that in the original region whence the pioneers sprang. The differences might be entirely in physiology or in habits, suited to the new surroundings. Brooks (1940) and Kendeigh (1945) describe differences in nesting habitats chosen by certain species of warblers indicating difference in habits without racial variation; but such cases are conspicuous because of their rarity. Usually the variations in physiology and habits are accompanied by alterations in color, size, or bodily proportions.

If the two populations are enough different so that individuals may be readily separated we call them distinct races or subspecies. Thus, the eastern ruffed grouse inhabits the broad-leafed woodlands near the Atlantic coast, and farther north in the evergreen forests of southeastern Canada lives another race, the St. Lawrence ruffed grouse. The intermediate zone between any two regions occupied by different races usually will contain populations intermediate between the two races, as expected from the blending of hereditary characters through interbreeding. Furthermore, in each of the two distinct races, there may be occasional individuals which appear more like the other race. This is to be expected in populations having a common ancestry, just as there are "throw-backs" quite different from the mode among domestic breeds of animals.

In considering the above described

natural spread of populations and its role in race formation, we may fail to realize the great length of time usually consumed in occupation of new territory. Nature is an extraordinarily patient wildlife manager, not concerned with fiscal budgets or demands of impatient sportsmen for quick results. A human life span is but a moment as compared with the time required for various plants and animals to become distributed as they are today on this continent. Furthermore, for most species, there probably are places in the world environmentally suitable for successful occupation by them, but which they never reach because of formidable geographic barriers. Occasionally these barriers are passed, either accidentally or through human aid, and the species may spread very rapidly in the new area, as did the English sparrow, starling, and ring-necked pheasant when helped across the oceans to North America. Such invasion of new territory requires no evolutionary change in the species. It is preadapted to the environment. It is probably significant that the ring-necked pheasant, the racial stock of which came chiefly from eastern China, has flourished best in the grain belts of the Middle West and Northwest, areas presumably closely approximating the conditions of its highly agriculturalized ancestral home. In the Shanghai region, whence imported pheasants likely came, the climate is similar to that in the corn belt of the United States. Twomey (1936: 124) shows by climographs that the temperature and rainfall of the areas in which such aliens as the Hungarian partridge and the skylark have become successfully established in North America are similar to the regions in the Old World from which these species were imported. Any differences which may be evolved by the species in North America, portions of which were occupied rapidly after introduction, would be the result of geographic isolation from the Old World stock. This, however, should not be confused with the process discussed in this paper, of differentiation through adaptation. That geographic isolation alone can bring about differentiation is amply demonstrated by the spectacular variation of birds on many islands of the Pacific Ocean, where geographic barriers are much more marked than ecological differences. In continental areas geographic barriers are not as effective, and ecological segregation is more obvious.

If geographic isolation were the most important factor in producing variation, the most widely separated races in a chain of differentiated populations should be most different from each other. Such, however, is not always true; but is more likely to be true if the geographical separation is accompanied by continued divergence in environment. If, on the other hand, the more distant portions of the range tend environmentally to be more like the region at the opposite end than the intervening territory, the characters of the widely separated races often converge. This tendency is dramatically demonstrated in the similarity of the race of ruffed grouse of the St. Lawrence River basin to that of northern Idaho, and the resemblance of the ruffed grouse of the Appalachian Plateau to that of the west slopes of the Cascades in Oregon. In both cases the

two regions are much more alike in climatic conditions than the intervening areas which support races of ruffed grouse entirely different from those on opposite sides of the continent.

In some instances the differences between two extremes of a progressive series showing racial variation are as great as would be expected in two distinct species. In fact we would not hesitate to call them distinct species were it not for the complete chain of interbreeding and intermediate populations which connect them. There is such a chain of populations in the song sparrows between the small pale reddish race of desert marshes in the southwestern United States and the large grayish birds of the virtually arctic Aleutian Islands. Almost as great a difference exists between the colorful deep chestnut ruffed grouse on the humid Olympic Peninsula in Washington, and the pale gray grouse occupying the timberline region of interior Alaska and northwestern Canada. Should the connecting populations be destroyed we would be justified in calling the remaining widely divergent races two distinct species.

There is reason to believe that most species and races of North American birds originated somewhat as follows. First, there was differentiation by gradual progressive steps in response to changing environment. Then came isolation and further differentiation until such great physical and physiological, and possibly psychological, changes were wrought as to discourage interbreeding even when the two populations again met through reinvasion of the intervening territory. The two varieties then remained distinct species, as apparently happened with the Canada and cackling geese. Thus different races of birds are in no way different from distinct species, save in the degree to which they have become differentiated from the original stocks (Dobzhansky, 1941: 155; Mayr, 1942: 362–378).

SIGNIFICANCE OF RACES TO MANAGEMENT

Of what practical significance are the above facts to wildlife management? No intelligent wildlife manager ignores the difference between species of birds in his management practices. Too often, however, differences between races have been ignored, usually with unfortunate results. Thus, repeated attempts have been made to introduce certain races of game birds into areas within the normal range of other races. Phillips (1928) and Bump (1941: 409–420) have summarized many of these. The usual result is that the birds are so poorly adapted to the new environment as to die within a year or so, leaving no trace of the introduction. This happened when Alberta ruffed grouse were introduced into Ohio, New York, Washington, Maryland, and Pennsylvania, and when prairie chickens were transplanted to the range of the eastern race (heath hen) in the Atlantic states. Many other similar failures could be enumerated. Phillips (1928: 3) has summarized the types of responses exhibited by species introduced into new environments which eventually fail to become established, as follows: (1) quick and complete disappearance; (2) lingering, but failing to breed; and (3) survival, but gradual decline over a period of years with final complete

eradication by unfavorable weather or other factors. Leopold (1933: 87) elaborated on the types of failure mentioned by Phillips and added two types of success: (1) an initial vigorous spreading followed by partial decline, and (2) prompt and vigorous spreading with complete establishment. Phillips (1928) rightly points out that the actual causes of failure to survive are usually so obscure as to go undetected, and much more thorough investigation of the causes of these failures would be profitable. An example of the type of work which should throw much light on the limiting factors to survival is that described by Kendeigh (1934): careful studies of the effect of climatic factors on the physiology of the species, together with the effect of biotic interaction and competition.

If any individuals of a native race are already present and the introduced foreign stock survives long enough to interbreed with them, the progeny presumably will be less well adapted to survive than offspring of pure native stock which has developed through long selective breeding under those particular environmental conditions. A. S. Leopold (1944) has shown rather conclusively that wild turkeys in Missouri crossed with domestic stock produce offspring much less able to survive under natural conditions than the pure native stock. This indicates a heritable factor in the wild birds which fits them for life under conditions in nature; the domestic birds, derived from a different race, have been altered further by artificial selection. During this process they have lost the physiological and psychological ability to cope with conditions which are successfully met by native wild turkeys. Artificially propagated stock of any game species is likely to have lost heritable characters of "wildness," or others which fit the birds to life under natural conditions—this because of the lack of natural selection under the artificial conditions of captivity. It would seem evident, therefore, that artificially propagated stock is not as satisfactory as wild material for purposes of introduction.

Of the many attempts to transplant American birds of one race into the range of another race the bobwhite quail (*Colinus virginianus*) seems to be the only species which has attained any degree of success. Even in this bird the reports of success are not entirely conclusive. Stoddard (1932: 480) reports that of 2,516 banded Texas bobwhites (Mexican quail), liberated during his studies in Georgia, the percentage of returns in birds killed by hunters in succeeding years compared unfavorably with banded native stock taken in the same territory, particularly in the second and third years after liberation. Phillips (1928: 27) has indicated that bobwhites have been introduced into New England from so many different sources and over so long a time that the indigenous stock now probably is extinct. Restocking was particularly active there after the severe winter of 1904–05, which decimated bobwhites all over the northern states; and that period probably marked the end of the big northern birds best suited to the rigorous climatic conditions of New Hampshire, Vermont, and Maine. The opposite of this situation seems to have prevailed elsewhere. Great numbers of bobwhites from northeastern Mexico

(*texanus*) and the southeastern states (*virginianus*) have been introduced into Pennsylvania and Maryland, yet large series of specimens from those states (in the U. S. National Museum) are closer to the ancestral stock (*marilandicus*)[1] than to the introduced types. Definite traces of both *texanus* and *virginianus* characters are noticeable however, in some specimens from the northeastern states, as Phillips has remarked. How long these foreign characters will persist in a population after introductions cease remains to be determined in most instances. It seems questionable that the characters of the native stock would often be entirely swamped out, as Phillips believed to be the case in New England. On the contrary, the selective nature of any characters developed by the native stock would seem to have an advantage tending to aid their perpetuation. This was pointed out by Stoddard (1932: 488), who noted a protective color advantage of native Georgia stock over introduced "Mexican quail." He also found it difficult to detect infusion of *texanus* blood into *virginianus* beyond the first cross. About 5,000 Mexican birds were released during a 5-year period over 200,000 acres in Georgia already well stocked with native birds; yet a few years later infusion of Mexican quail blood was noticeable only in the places where the imported birds had been released in considerable numbers. Stoddard now states (letter, 1945) he can detect little or no trace of the introduced birds among the several hundred examined annually.

It seems obvious that stocking with a foreign race is a waste of time and money, at least while any of the original inhabitants of a region still survive. Instead of introducing new birds of a strange race, the original occupants of the region should be given every encouragement to increase their population to the carrying capacity of the region which their hereditary constitution permits them to occupy; then all would be done that could be expected of a scientific management program. This seems to be the recommended practice of most modern wildlife managers.

If all of the original inhabitants of a certain bird species have been killed off in a region, and it is desired to restore the species, or if it is desired to stock a region in which the species never occurred, what procedure would be most likely to succeed? From the foregoing, introduction may be successful if stocks can be obtained in other regions with environmental conditions similar to or identical with the area where stocking is desired. The difficulty is to know in advance whether the two regions are similar enough. This might be determined by a thorough study of all environmental factors. It would be the more difficult but surer method and the only one possible for areas in which the species is not known to have occurred naturally.

[1] The racial divisions and nomenclature of the bobwhites referred to here differ from those of current standard publications, and are the result of recent unpublished studies by the writer. *C. v. mexicanus* is the race inhabiting the greater part of the eastern United States; *virginianus* is confined to the southern Atlantic coastal plain; *marilandicus* occupies the northern Atlantic seaboard; *floridanus* is restricted to peninsular Florida; *taylori* inhabits the Great Plains south to northern Texas; and *texanus* occurs in southern Texas and southward into northeastern Mexico.

There are innumerable failures in transplantation of birds without regard to similarity between the habitat of origin and place of introduction. The Chukar partridge in Missouri is a case recently studied (Nagel, 1945). Stock (reputedly of the race *Alectoris graeca chukar*) presumably from the southern Himalaya Mountains, was liberated in numbers in a variety of regions and habitats in Missouri. The birds wandered widely and failed to maintain their original numbers. It was concluded that the ecological conditions were not enough like the original home of the introduced stock, but that birds of some other race of this widely ranging and exceedingly plastic species possibly would be satisfactory.

There is one seemingly successful instance of bobwhite introduced into a region where the species formerly did not exist. According to Phillips (1928: 27) stock was introduced into Washington from Kansas and subsequently the species has done particularly well in the more arid plains country east of the Cascades, whence birds have been transplanted into Idaho. Recent specimens from Washington, Oregon, and Idaho seem to be predominantly of the pale *taylori* type, which evolved in the Great Plains of Nebraska, Kansas, Oklahoma, and eastern Colorado, and is the stock which would be expected to be most suitable for the similarly arid situation of the northwestern states. In this case it would seem that intelligent, or at least fortunate, choice was made.

If a species formerly occurred in a given region and specimens are available for identification, the most practical method would be to select stock of the same race as the original inhabitants of the area to be stocked. The difficulty here is that birds of two regions may appear similar enough to be considered the same race, yet may have small physiological differences (not reflected in outward appearance) in response to slightly different environmental conditions which would render them unsuited to survival in another region. In such a case, trial and error is the only method possible. The chances of success would seem greater than if stock were selected from an obviously different race which almost certainly would have physiological characteristics unsuited to the environment of another race.

This is where the museum taxonomist may be helpful in wildlife management. Specially trained ornithologists with access to the necessary reference collections can distinguish racial differences in birds, and by plotting their distribution can correlate these races with the distribution of ecological communities studied and plotted in the field. Museum specialists know that many named races of birds, and some populations not sufficiently distinct to be named, are distributed in rather close agreement with regions characterized by distinctive climatic conditions, of temperature, rainfall, and evaporation. Major climatic regions are usually recognized at a glance by the conspicuous forms of vegetation, but thorough analysis of all forms of life is necessary to distinguish their finer subdivisions. These climatic regions with their ecological subdivisions have long been known as life zones. The major characteristics and composition of life zones and their com-

ponent ecological units have been worked out in a general way. More thorough and detailed description of the major biogeographical units, and particularly of their component biomes, on the basis of exhaustive ecological studies correlated with the racial variation of the animal life which inhabits them is needed. In fact such studies are essential to sound wildlife management.

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AGE AND SEX CRITERIA AND WEIGHTS OF CANADA GEESE[1]

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This study was conducted at Horse Shoe Lake, Alexander County, Illinois, and aided by observations on a large captive flock of Canada Geese (*Branta c. canadensis*) at Bright Land Farm, near Barrington, Cook County, Illinois. The Horse Shoe Lake area has been owned and operated as a refuge by the State of Illinois since 1927. In 1931 the State Department of Conservation built a permanent dam at the outlet of

[1] Acknowledgments are due as follows: for aid and advice at Horse Shoe Lake to U. S. Game Agent Paul S. Smith; for help on the manuscript to Arthur S. Hawkins, Margaret B. Hickey, Joseph J. Hickey, and James S. Ayars; for advice on statistical methods to Prof. H. D. Landahl, Department of Mathematical Biophysics, University of Chicago; for aid in the field and the library to Nina L. Elder; and for cooperation in work at Horse Shoe Lake State Game Refuge by the Illinois Department of Conservation, and especially by Mr. and Mrs. C. E. Laughery. Studies at Bright Land Farm during the spring and summer of 1940–43 were by permission of the late A. L. Eustice and Mrs. Eustice; Carlton A. Beckhart cooperated in observations there.

the lake to maintain a fairly constant water level.

Horse Shoe Lake is dotted with cypress trees and encircles some 1,300 acres of rich farm land on which corn and wheat are raised as food for the geese. The first geese arrive during the last week in September and their numbers gradually increase until about 50,000 are present in November and December. Most of them remain throughout the winter, but scatter out as the need for food demands.

Arthur S. Hawkins began the study in 1941 and developed a successful trap for geese. The writer continued the work from December 1941 until March 1942, and from September 1942 until March 1943.

Two large traps were used, being baited with corn, camouflaged with corn stalks, and operated by a string from a blind. This frequently necessitated as much as 100 hours of vigilance before a catch was made, but up to 200 geese were captured at once. The age, sex, and weight of each were determined at the trap as the geese were handled for banding.

The many hunting clubs close to the Refuge facilitated inspection of hunters' bags, and during the 60-day shooting season in the autumn of 1942 over 750 geese were examined—these represented 10 per cent of all killed in the region that year. These birds were weighed and the cloaca examined for age and sex criteria. The more prominent "wing spur" or knob on the carpus of older birds was noted but no objective measurement was devised. This criterion for aging was suggested by Brooks (1914) and Phillips (1916). The latter also mentioned that the roughness of the feet increased with age, but I made no observations on the latter feature.

An occasional Hutchins goose (*Branta c. hutchinsi*) was present, but most of the population was of the common Canada goose (*Branta c. canadensis*).[2] One hundred birds of all ages and sexes were measured; none was found that could be considered a lesser Canada goose (*Branta c. leucopareia*). An occasional bird suffering from lead poisoning was within the weight range of the last named, but measurement of the culmen always proved the bird to be too large for that subspecies as delimited by Taverner (1931).

Throughout this paper, the following terms are used to designate the age classes: *First-year*, *second-year*, and *third-year* refer to birds known to be in these respective years of life. Since the exact age of most live birds handled was not known they are referred to as either *juvenile* (in their first year by criteria described below) or *adult* (second or subsequent years).

WEIGHT

The weight of Canada geese is a common subject of discussion among hunters. Many an enthusiastic wildfowler brought his "15 pounder" to our checking station and was surprised that it did not exceed 9 pounds.

In 1942 and 1943, a total of 2,179 Canada geese were weighed during bag inspections and banding studies. Only six exceeded 10 pounds, the largest weighing 11 pounds 9 ounces; all six were males. This limit agrees

[2] Corresponding to *Branta c. interior* of Todd (1938), a proposal not accepted by the American Ornithologists' Union (1944).

closely with the figures of other workers in the eastern United States (Leffingwell, 1888; Bruette, 1929; Phillips and Lincoln, 1930; Miner, 1937; McAtee, 1941; Pearson, Brimley and Brimley, 1942). The only large sample reported in literature seems to be that of Jack Miner (1937), who banded 16,775 geese; he found only one goose per hundred to exceed 11.75 pounds, and only one in a thousand to exceed 12 pounds. Pinioned birds kept 10 years in captivity by him occasionally reached 14 pounds in weight. DuMont and Swenk (1934; 1935) also discussed the weights and measurements of 356 geese (*Branta*) taken in Nebraska in 1884–86. As their analysis clearly shows, several subspecies were represented and only 57 specimens with weight data recorded could be ascribed to the common Canada goose (*canadensis*). The latter ranged from 5.5 to 13 pounds, and six (5%) exceeded 10 pounds—a greater proportion of heavy birds than in the studies here reported. Their heaviest bird weighed 13 pounds.

The maximum weight of Canada geese has been discussed by Mershon (1925) and McAtee (1944), who point out that the extremely large geese (13 to 19 pounds) reported in the past probably comprised a distinct race. With few exceptions those large birds were taken on the Great Plains. There is also a statement by McKinley (1885), that stragglers then remaining in Nova Scotia until Christmas "reach the extraordinary weight of 18 pounds." Forbush (1925) gives the weight range of Canada geese as "8–14 pounds," but the source and size of his sample are not given. The upper limit may have referred to captive birds.

AGE AND SEX DIFFERENCES

Only the weights of the 1,028 live birds handled in banding are included in this discussion—and in that following on the winter loss in body weight. Weights of 390 additional birds from the previous year of banding were available and of 761 other birds from bag-inspection studies, but these were excluded for fear they would introduce new variables—differences between years and sampling methods.

The frequency distributions of the age and sex groups (Fig. 1) indicate that males are heavier than females and adults are heavier than juveniles, but before the end of the hunting season (December 15) juvenile geese of either sex occasionally exceed the average of the adults, which is exactly 8 pounds. To discover whether this difference was significant, the weights were subjected to statistical analysis.

Table 1 gives the data and standard deviation[3] for each age and sex group in the months the birds spent on the wintering ground (except October, when the sample was inadequate). There

[3] Standard deviations were determined directly by finding half the difference between the 84th and 16th percentile weights. The significance of the differences of the means was determined by finding their critical ratios (ratio of difference of the means to standard error of the means) by the formula:

$$\frac{M_1 - M_2}{\sqrt{({}^{\sigma}M_1)^2 + ({}^{\sigma}M_2)^2}}$$

where M = mean and ${}^{\sigma}M$ = standard error of the mean. Values of the probability of occurrence for critical ratios were from Hodgman (1941, p. 201). In the present paper any critical ratio greater than 3 (chances 1:370) is considered significant; and any ratio greater than 4 (chances 1:16,000) highly significant.

TABLE 1.—BODY WEIGHTS (IN POUNDS) OF 1,028 CANADA GEESE TRAPPED AT HORSE SHOE LAKE, ILLINOIS.

	Month	MALES Number	Weights Average	Minimum	Maximum	Standard deviation	Total lbs.	σ	FEMALES Number	Weights Average	Minimum	Maximum	Standard deviation	Total lbs.	σ
Juvenile	Nov.	65	7.30	5.56	8.56	.65	474.31	.92	41	6.63	5.2	7.9	.55	271.81	.61
	Dec.	91	7.82	5.56	9.25	.77	712.065		77	6.77	4.6	8.2	.64	521.81	
	Jan.	61	7.26	5.94	8.69	.61	443.25		57	6.40	5.1	7.9	.53	364.56	
	Feb.	69	7.31	5.06	8.63	.81	504.69	.73	57	6.31	5.3	7.6	.76	359.56	.56
	Mar.	46	7.41	5.88	9.00	.83	340.872		49	6.48	5.2	7.8	.84	317.749	
		332	7.455	5.06	9.25	.85	2475.187		281	6.53	4.6	8.2	.578	1835.489	
Adults	Nov.	42	8.60	6.5	10.0	.80	361.0	.71	36	7.33	5.7	8.8	.64	263.81	.76
	Dec.	41	8.94	7.2	10.6	.62	366.375		40	7.23	6.0	8.5	.88	289.125	
	Jan.	36	8.01	7.1	9.5	.68	288.375		35	6.77	5.3	7.9	.70	236.90	
	Feb.	51	8.12	6.2	9.5	.74	414.430	.72	31	6.91	6.0	8.4	.68	214.24	.64
	Mar.	46	8.24	6.9	9.7	.75	378.997		42	6.97	5.6	7.8	.57	292.75	
		216	8.38	6.2	10.6	.81	1809.177		184	7.05	5.3	8.8	.70	1296.825	

is a highly significant difference between the weights of juveniles and adults of each sex and between the weights of males and females at any age (Fig. 2).

The weights of Canada geese in California as reported by Moffit (1931) exceed those of Illinois birds, but the difference between the sexes is similar because his "fat males" average 10 to 12 pounds and females in good condition 8 to 10 pounds. Such a difference was not shown by the small sample (57 birds) of Nebraska *Branta c. canadensis* recorded by DuMont and Swenk (1935).

WINTER LOSS IN WEIGHT

Canada geese at Horse Shoe Lake lost weight shortly after the close of the hunting season in mid-December. All crops providing food for the geese then had been exhausted for several weeks and the weather was cold. Since the geese were not maintaining their weight, despite the shelled corn being scattered,

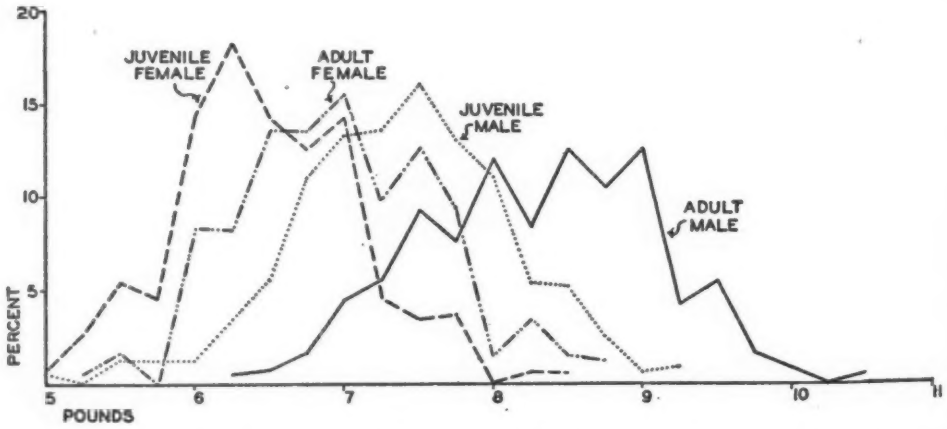


Fig. 1. Frequency distribution of weights in 1,028 Canada geese trapped during winter at Horse Shoe Lake, Illinois.

the carrying capacity of the Refuge seemingly had been exceeded. To determine whether the apparent weight loss was statistically significant, the data for each age and sex group were divided into two lots (Nov.–Dec. and Jan.–March). The means and standard deviations for each group are given in Table 1 and the differences are shown in Figure 2. Each age and sex group showed significant loss in weight, whereas the differences between the ages and sexes remained approximately constant.

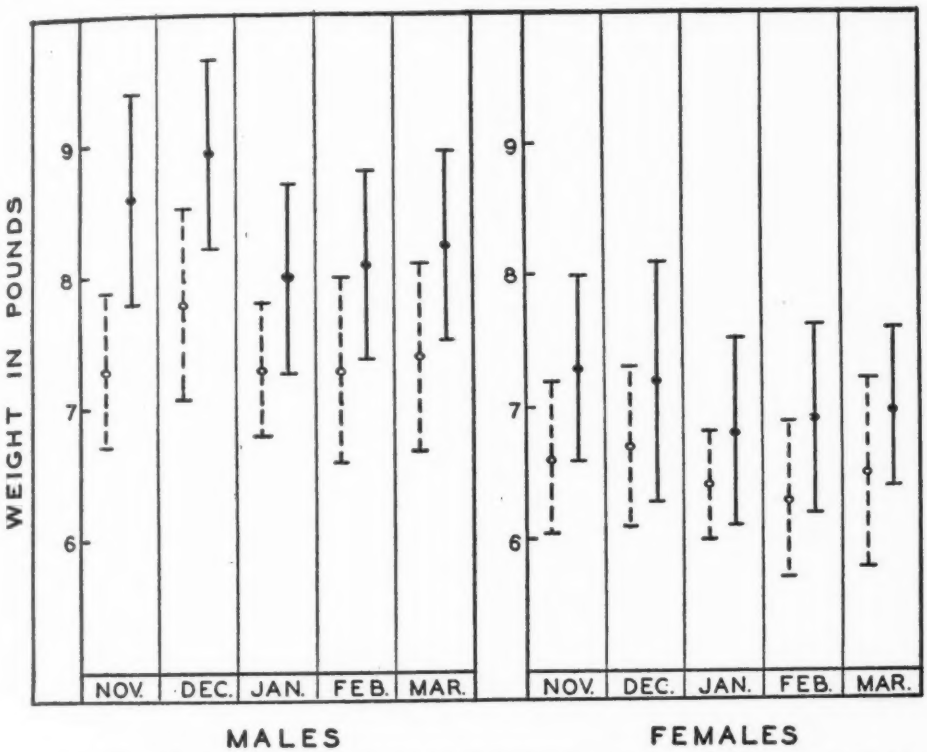


Fig. 2. Monthly weight trends among 1,028 winter-trapped Canada geese. *Broken lines*, range in weight of juveniles ±one standard deviation; circle indicates mean. *Solid lines*, similar data for adults.

There are few published data on seasonal changes in weight of waterfowl. Bennett (1938, p. 5) gives weights of 47 bluewinged teal equally divided among the four seasons. Except for females ready to lay, the heaviest birds of both sexes were found on the wintering ground. Passerine species have been more thoroughly investigated. The literature on this subject is well reviewed by Nice (1937) and by Baldwin and Kendeigh (1938), who agree that in the migratory species studied, maximum weights are reached in winter or early spring just prior to migration. Further evidence has been added by Nice (1938), Blanchard (1941), and Becker and Stack (1944). Recently

Wolfson (1945) has demonstrated clearly that migratory members of any passerine species gain weight prior to migration. These energy supplies are necessary as indicated by Blanchard (1941) who discovered that the large stores of fat (25% of body weight) acquired by white-crowned sparrows on the wintering area were used entirely during the northward migration.

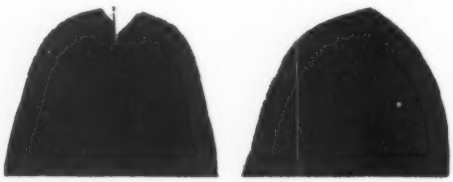


Fig. 3. Tail feathers of Canada geese. *Left*, juvenile with notched tip; *right*, adult.

The teal studied by Bennett likewise lost all weight gained on the wintering grounds in Mexico by the time they reached Iowa. In spite of the interesting evidence by Gerstell (1942) that pheasants experimentally fasted showed increased fecundity and fertility, the opposite is probably true for migratory species. A migratory species that suffers great loss of weight on its wintering ground probably will not reach the breeding range and reproductive season in the best of condition. In a young goose this may be a factor in determining whether the bird will start to breed in its second, third, or fourth year of life.

THE TAIL

Of all plumage criteria to distinguish juvenile Canada geese from birds in their second or subsequent years, the tail has proved the most certain and most convenient. The characteristic notches at the tips of juvenile tail feathers are shown in Figure 3. Kortright (1942) gives a diagram of their appearance in waterfowl generally. This criterion was shown to me in 1938 by H. Albert Hochbaum who used it continually at the Delta Duck Station. The dull brown of the flight and tail feathers in a juvenile is in sharp contrast to the glossy black in older birds as shown in Plate 6, B. The disparity in length shown in that figure is unusual.

MOLT

The less rapid loss of juvenile tail feathers in geese as compared with ducks has been pointed out by Kortright (1942), who says, "In geese and swans the juvenile tail is not replaced by adult feathers until late autumn or early winter." The molt in geese at Horse Shoe Lake was much slower, involving their entire stay on the wintering grounds. In fact 10 per cent of the 923 immature geese handled in winter had not begun molt of the juvenile tail, and some handled in March just prior to migration still had complete juvenile tails. One first-year male caught February 6, 1942, had the outer pair of juvenile tail feathers only half grown. This is a continuous winter molt, and not an arrested molt as Leopold (1943) describes for turkeys. It was shown by numerous geese found with blood quills during each winter month. Retrapped birds showed an increase in number of adult tail feathers throughout the winter.

The other extreme was represented by a juvenile female taken November 23 with 16 adult feathers and only one

juvenile feather on each side (18 is the usual number in an adult).

Irregularity in the tail molt is not limited to the young, as seven adults had a varying number (3 to 15) of the previous year's rectrices not replaced. These feathers were easily distinguished by their lighter color as a result of fading. A few adults each month had one or more partly grown tail feathers (blood quills) with adhering basal sheaths, indicating their growth had just been completed.

All feathers of the juvenile tail are not as clearly notched at the tip as shown in Fig. 3. The depth of notch is greatest in the center tail feathers, but can seldom be seen in the outer few feathers; this may include as many as five on each side. In such individuals only the central three or four pairs are notched. Progression of the tail molt in geese is from the center pair outward (centrifugal), and an individual with only the four central pairs of feathers notched would show no notches when the molt was less than half completed. Age in such individuals is recognized by the brown color and lack of gloss of the outer feathers.

Juvenile geese with molt of the rectrices complete were not found until March and then only in small numbers; they actually were immatures, as determined by cloacal characters.

NUMBER OF FEATHERS

For many years the number of tail feathers in geese of the *canadensis* group was considered as diagnostic of subspecies. Swarth (1913) proved this to be unreliable, as the number is extremely variable in all races. It may be assumed that prior to the appearance of Hochbaum's paper (1942) the age of specimens was not determined by cloacal characters.

It seemed important, therefore, to learn whether the variations discussed were due to age or sex. The number of tail feathers was determined for all geese handled in banding and in bag-inspection work. Birds with obviously damaged tails, and juvenile geese with incomplete tails or with any adult feathers, are not included. Only 10 per cent of the juvenile geese handled are included in this part of the discussion, as the balance were undergoing molt of the tail. Until more is known of the exact nature of the tail molt, it is not safe to assume that each adult tail-feather follicle was previously occupied by a juvenile feather. Leopold (1943) has shown this not the case in turkeys.

The percentage distribution of geese with 14–19 tail feathers in each age and sex group (Fig. 4) shows no great difference between the groups. Juveniles have the maximum number (19) as frequently as adults. Of the juvenile geese examined, 19.4 per cent had 14 or 15 tail feathers while only 8.1 per cent of adults were in this group. Of all geese examined, 86 per cent had 16 to 18 tail feathers; 77 per cent of juveniles were in this class and 89 per cent of adults. There is no real difference between the sexes at either age level so far as the above groupings are concerned; but adult males had 18 tail feathers more frequently (45%) than any other age or sex group.

OTHER PLUMAGE CRITERIA

Bent (1925) and others have mentioned that young geese may be dis-

tinguished from adults by a brownish cast on the head and neck, by the brownish white of the cheek patches, and by the less clearly cut margins of the black areas. These differences were seen in the captive flock at Bright

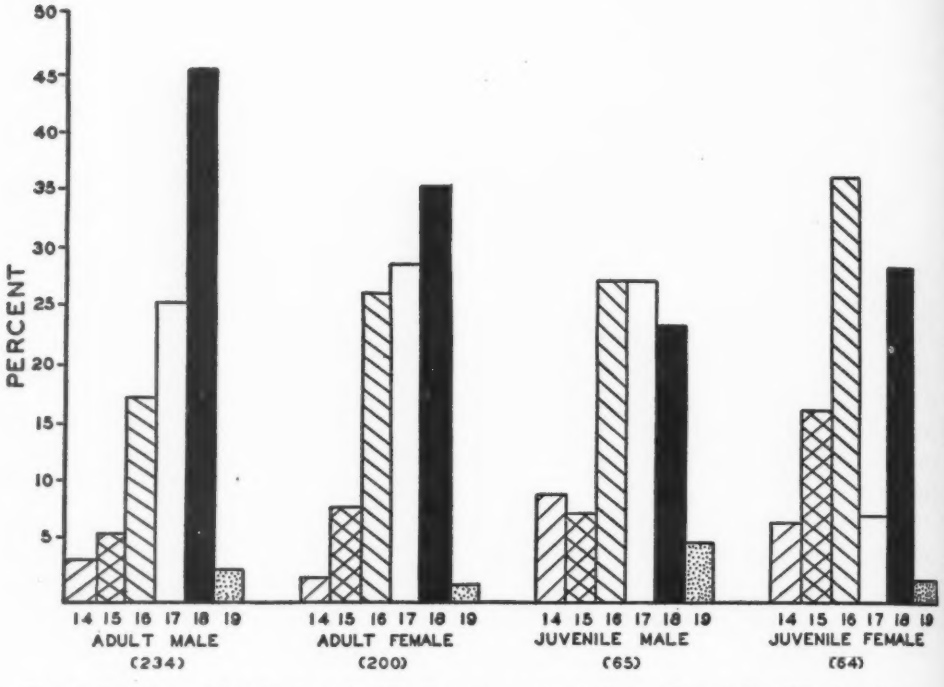


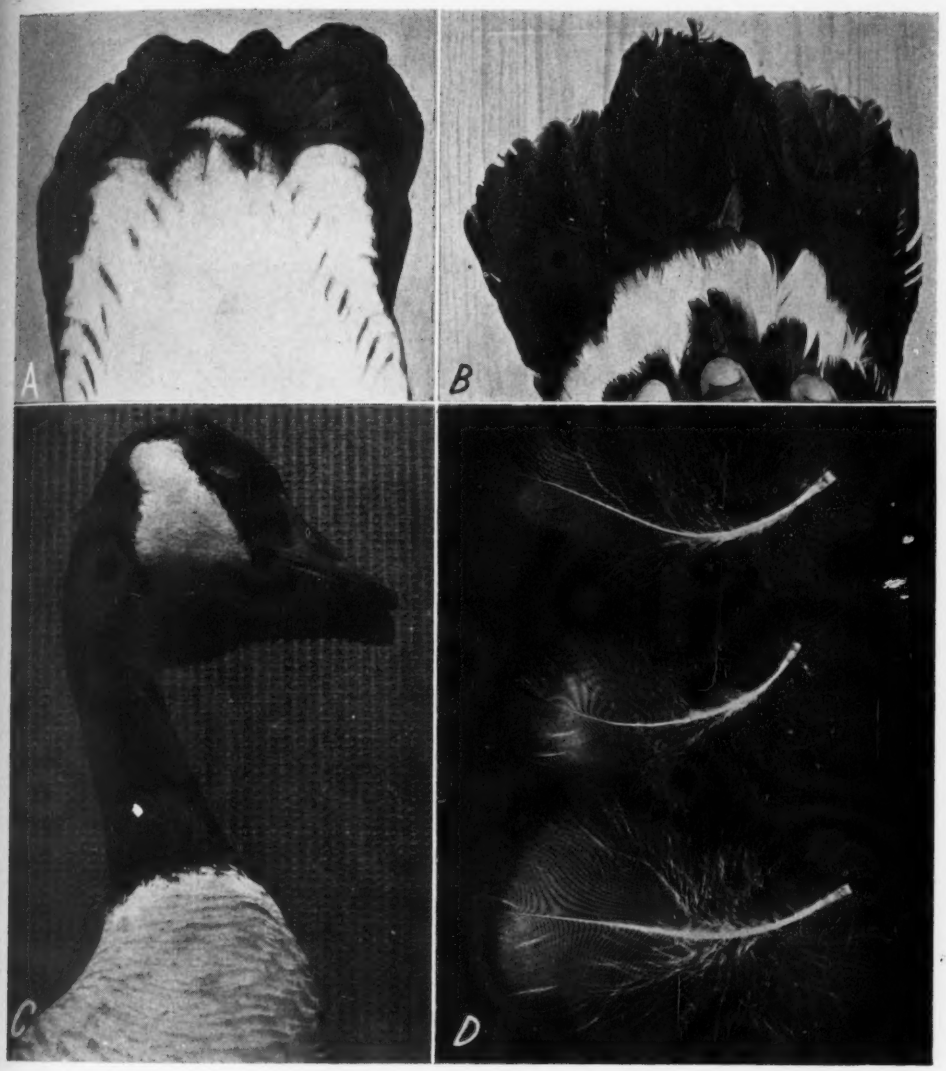
Fig. 4. Numbers of tail feathers in 563 Canada geese at Horse Shoe Lake, Illinois; of the juveniles only those not in process of tail molt are included.

Land Farm during August, but were not present in migrants arriving at Horse Shoe Lake during October and November. Only rarely could a bird be so distinguished on the wintering ground. Other plumage variations easily recognized in the field were frequent enough in occurrence to be examined as possible age or sex criteria.

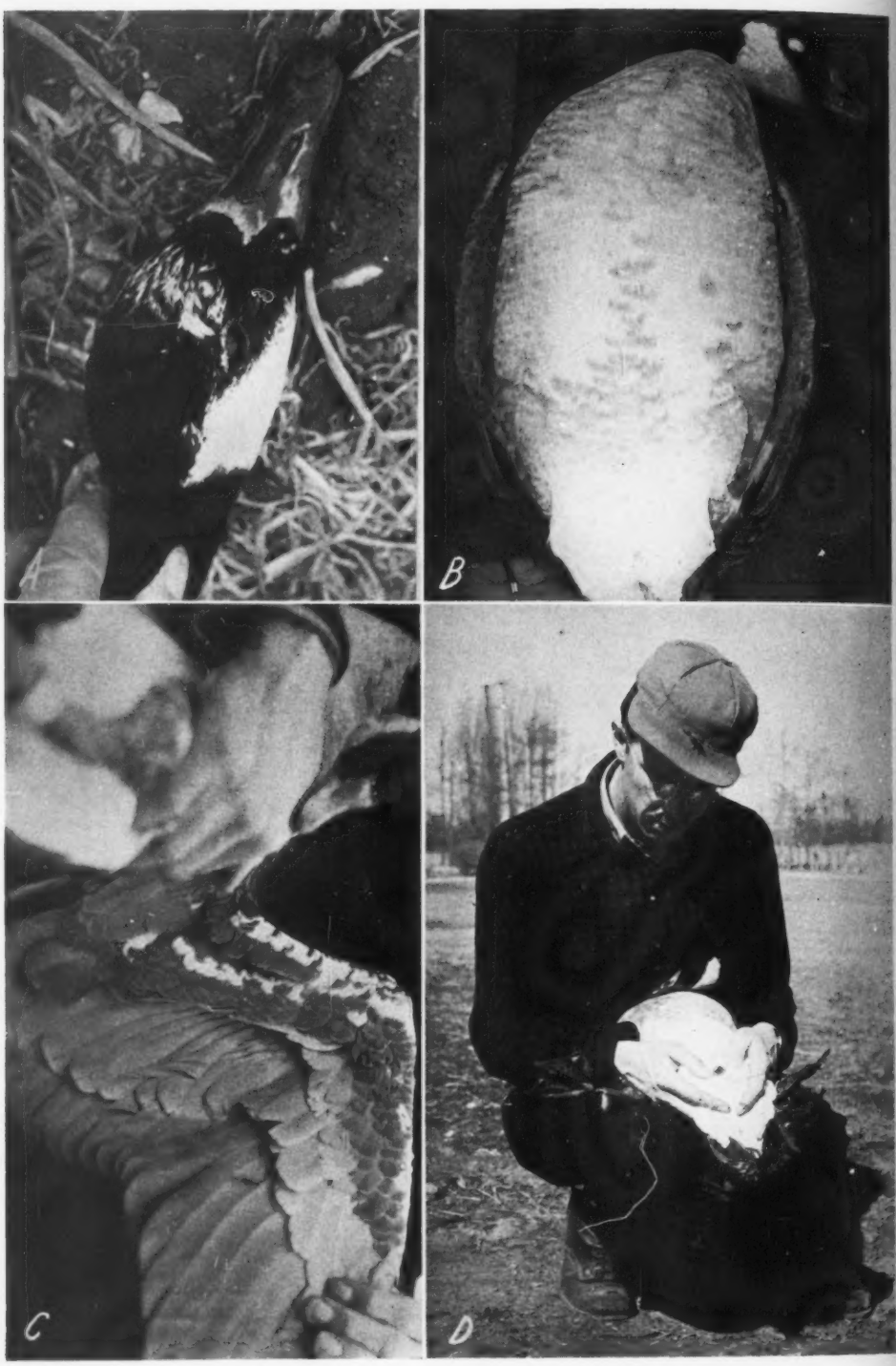
During banding in the winter of 1942–43, a total of 1,028 geese were examined for the following plumage variations: (1) white collar, a crescent or ring of white feathers at the lower margin of the black neck; (2) white wing feathers, frequently scattered along the margin and under surface of the wing; (3) white patches on the head, often clearly circumscribed on the forehead or crown; (4) melanistic tail coverts, both upper and lower; (5) light-colored breast, pale enough to be noticeable but not the pure white of an albino; (6) retarded molt, juvenile plumage persisting on breast and belly; (7) gloss of tail and primaries; and (8) number of body feathers.

WHITE COLLAR

This plumage variation is shown in Plate 6, C. Formerly it was considered of taxonomic significance and gave rise



Canada geese in Illinois. *A*. Melanic under tail coverts. *B*. Tail of juvenile in process of molt (March 3, 1942). *C*. Goose with white collar at base of neck. *D*. Typical breast feathers: juvenile at top, post-juvenile at center, adult at bottom.



Canada geese in Illinois. *A.* White markings on crown. *B.* Juvenile with retarded post-juvenal molt (Jan. 27, 1943). *C.* White under-wing feathers of an adult. *D.* Method of holding goose for cloacal examination.

to the now archaic common name of "white-collared goose" for *Branta c. leucopareia*. Swarth (1913) and Taverner (1931) showed this character is not associated with specific or subspecific groups. A white collar is three times as frequent in older birds as in first year birds (Table 2), but is not of frequent enough occurrence to be diagnostic of age or sex. Geese with this plumage variant were found in Illinois by Nelson in 1876.

TABLE 2.—PLUMAGE VARIATIONS IN WINTERING CANADA GEESE, HORSE SHOE LAKE, ALEXANDER CO., ILLINOIS, 1942–43.

	Adult		*Juvenile*	
	Male	*Female*	*Male*	*Female*
Birds examined	217	187	337	290
Percentages with:				
White collar	15.2	17.9	3.3	6.2
White head areas	3.2	1.6	5.8	3.4
White wing feathers	32.2	37.5	1.5	1.4
Melanic tail coverts	15.2	15.2	18.1	19.6
Light-colored breast	9 birds			
Retarded molt			3 birds	3 birds
Tail and primaries	glossy black		dull brown	
Body plumage	firm and dense		less dense	

WHITE WING FEATHERS

These were present in one-third of all the adults handled (401) and vary from a scattering of 8 or 10 feathers to considerable areas (Pl. 7, C). Of the 627 juvenile geese, only nine showed any white in the wing and none had white on more than three feathers. In general, areas of white are present only in birds more than one year of age.

WHITE HEAD AREAS

Conspicuous areas of white on the head or neck (Pl. 7, A) are infrequent, being present in only 3.1 per cent of the population sampled, and cannot be associated with any age or sex group.

MELANIC TAIL COVERTS

Any pigment in the white tail coverts stands out clearly when a goose is in hand (Pl. 6, A). Such pigmentation was found in 17.5 per cent of those examined, but was not associated with any particular age or sex. Such feathers are found in both juveniles and adults, as mentioned by Witherby (1939).

LIGHT-COLORED BREAST

Phillips (1910) states that variation in the whiteness of the breast feathers is not due to age. In this I concur, having found only nine such individuals in the 1,028 geese banded; these were not limited to any age or sex group. This light color is not to be confused with that due to persistent juvenile feathers, as explained below.

RETARDED MOLT

Plate 7, B shows a juvenile goose with light breast due to greatly retarded post-juvenal molt. Such light areas mark the presence of juvenile feathers that are smaller and with more rounded tips than the normal feathers of the first winter, and actually only half as wide as in an adult (Pl. 6, D). This difference in size and shape of the juvenile and adult breast feathers has been pointed out in many species of geese by Witherby (1939, III: 179–219) and Alpheraky (1905).

GLOSS

Brooks (1914) noticed a dull brownish cast of the rectrices and remiges of immature geese in sharp contrast to the glossy ebony black of adult birds. This

is particularly noticeable as the new rectrices are being acquired, when the contrasting feathers are viewed side by side in the same tail.

NUMBER OF FEATHERS

No actual feather counts were made, but in plucking many geese found dead on the Refuge it became obvious that, as suggested by Brooks (1914), birds in their first year are less heavily feathered than older individuals. The greater size, stiffness, and number of the body feathers on the adults make their plumage much firmer and more dense. The difference between first-year and older birds is great enough so that after handling many geese the examiner can usually identify an older individual during the hunting season by merely running his fingers through the plumage of the belly. How long this distinction persists through the year was not determined. Occasional autopsies of juvenile geese through the winter and spring showed many more body feathers being gradually acquired. This steady acquisition of feathers has been noted by Bent (1925) in Canada geese and by Alpheraky (1905) in the geese of Europe and Asia.

THE CLOACA

Hochbaum (1942) described means of using the cloaca and associated structures to distinguish age and sex in waterfowl. He was first to indicate the great convenience of this method for the field worker and the importance of refining the technique for each species of waterfowl.

Little seems to be known of the age at sexual maturity of Canada geese in the wild, and the sexes cannot be distinguished by plumage characters; hence it was of special importance to make a thorough study of the cloaca. The writer examined over 1,000 geese in hunters' bags and nearly twice that number of live birds. All of the dead and most of the live geese were seen at Horse Shoe Lake. The other live birds were in a large captive flock at Bright Land Farm. Examination of the latter was possible at all seasons and the birds were of known age, the young of each year having been distinctively color-banded. Observations on these captives were important in gaining technique and understanding, but conclusions based on them cannot be carried to wild populations without reservations.

METHOD OF EXAMINATION

The position in which a live goose is held for cloacal examination is shown in Plate 7, D, being similar to that described by Hochbaum (1942) for ducks but making additional use of the observer's thighs in restraining the bird. Firm and complete restraint is of utmost importance to both bird and investigator. If the means of holding a bird is not thoroughly learned, the examination of several hundred in a single day becomes particularly fatiguing, and the geese are more likely to sustain damage. The bird's legs are not held; their strength is such that restraint would be laborious for the operator and an added strain on the bird.

The operator's hands must be free for everting the cloaca, often a difficult process. Firm and even pressure is exerted downward and laterally with both thumbs. Much difficulty may be

experienced at first in many old birds because their cloacal musculature is strong. Increased pressure with the thumbs is to be avoided; slight shifts of the pressure posteriorly and anteriorly will bring the desired eversion. Skill cannot be expected until several hundred birds have been examined.

for spreading the cloaca and gives a clean cut when the end is inserted inside the anterior cloacal lip and drawn quickly toward the operator.

THE NAKED AREA

Upon first separating the cloacal feathers, a circular unfeathered area is

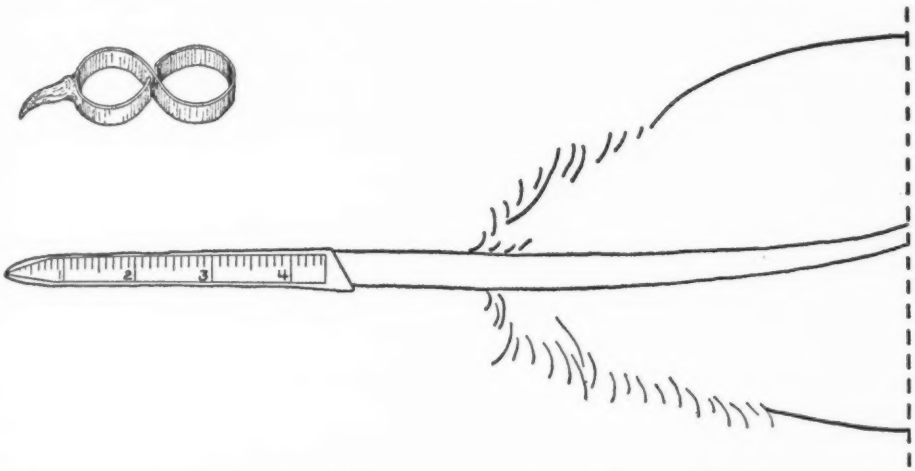


Fig. 5. *Above*, tool for cutting rim of cloaca to examine geese in hunters' bags for age and sex. *Below*, gauge for measuring depth of bursa of Fabricius.

Hochbaum (1942) suggested the need of an assistant in holding the large birds, but this is unnecessary.

To measure the bursal depth or to search the cloacal wall for the oviducal opening in dead birds, the anterior lip of the cloaca must be cut in midline so that it can be opened more widely. A knife or other sharp instrument can be used but a special small metal tool is more convenient for the purpose (Fig. 5, above). In use the little finger is inserted through the hole next to the blade and the "ring finger" through the other. Being worn like a ring, this tool is never mislaid during inspection of hunter bags; it leaves both hands free

seen, in the middle of which is the vent or opening to the cloaca. This is actually the outer surface of the cloacal wall. The dimension and color of this area change distinctly with age. In first-year birds the naked area is about 15 mm. in diameter, and in older birds 25 mm. or more. The color in juvenile birds throughout the summer, autumn, and winter is flesh pink. In March, just prior to migration, a few young geese were found in which the pink was distinctly tinged with blue black. Birds in their second year often had the same uniform pink coloration present during the first year; others showed all degrees of the bluish black coloring. Upon

everting the cloaca in the latter birds, the same sort of pigmentation was found on the papillae surrounding openings of the ureters into the cloaca at each side of the rectal opening.

From color-banded birds at Bright Land Farm it was determined that some geese in their third year still had the clear pink naked area of the juvenile while the remainder showed some degree of pigmentation. No pink cloaca was found in the fully adult group of that flock (4th year and older); all showed definite pigmentation, some being quite black (presumably those 10 years or more of age; the exact ages of the older geese were unknown).

Thus the naked area surrounding the vent, and the ureteral papillae within the cloaca, gradually become pigmented until the flesh pink color of the juvenile is eventually replaced by deep blue black. Because there is much individual variation in the rate at which the color is acquired and because all geese probably do not actually breed at the same age, this color criterion alone cannot be relied upon to place the goose in a definite age class. It is rather an index to physiological age. Preliminary experiments by the author indicate this pigmentation is under direct control of the sex hormones.

THE PENIS

The presence, mechanism, and function of the penis in different birds has been discussed by various authors (Owen, 1866; Gadow, 1887; Müller, 1908; Gerhardt, 1914; Liebe, 1914; Stresemann, 1928; Van Oordt, 1931; Benoit, 1936; and Groebbels, 1937). The well-developed copulatory organ of the drake was figured by Home (1802) and was thoroughly studied and illustrated by Liebe (1914). Hochbaum (1942) was first to point out to wildlife workers the value of this structure for distinguishing the sex and age of ducks and geese; he also stated, "preliminary studies of the Canada goose by Arthur Hawkins indicate that in this species there may be an intermediate stage of development in the penis and an intermediate stage of regression in the bursal characteristic of yearling birds." The present writer has continued this study with both live and dead geese.

When the cloaca of a goose is everted by the method described, the penis is seen as a spiraled organ arising from the inner wall of the left side. In first year birds it does not exceed 10 mm. in length, and resembles in size the exposed lead of a well-sharpened pencil; it is of the same pink color as the cloacal wall. In the second and subsequent years it is much larger and easily distinguishable from that in first year birds. In these older birds the corpus fibrosum ("firm basal sheath" of Hochbaum) has developed and fills most of the left half of the cloaca. After the cloaca is opened, continued gentle pressure causes the eversible part of the penis to slowly protrude 20 to 35 mm. from the firm basal part. As the penis spirals out, the sharp-pointed, transverse rugae can be seen; these are distinctly pigmented in old ganders. In such older birds, the internal apparatus for retracting the penis after eversion (muscles and ligaments described by Owen, 1866; Gegenbaur, 1878; Gadow, 1887; and Stresemann, 1934) becomes so well developed and strong that complete ex-

posure of the organ for examination is difficult.

Some males in their second winter have both the eversible and firm parts distinctly smaller than in the average adult, but many in their second winter have a penis fully as large and well pigmented as in older geese at that season of year. Such disparity in development of the copulatory organ probably is associated with the fact that not all geese reach sexual maturity at the same age. Neither the degree of pigmentation nor dimension of the penis therefore can be used on wintering grounds to separate birds in their second winter from older individuals.

THE CLITORIS

When the cloaca of a female is everted, a small protuberance is seen in the midline of the anterior wall. In first-year birds this may be 5 mm. long and 1 mm. in thickness, or may be barely discernible. In older geese it doubles in size, to a maximum length of 10 mm. As sexual maturity is reached, the tip becomes pigmented as do the penis, ureteral papillae, and external cloacal wall in males.

That this organ in female birds is the homologue of the penis and thus justifies the use of the name clitoris has not been experimentally proved; in fact, it is not mentioned in standard texts on comparative anatomy (Messer, 1938; Neal and Rand, 1939; Walter, 1939; Hyman, 1942). Owen (1866, p. 251), however, noted that the ostrich has a well-developed clitoris, with a groove like the penis of the male, and states, "a smaller clitoris exists in those birds of which the males have a well-developed intromittent organ." Stresemann (1934) concurs and apparently bases his opinion on embryological evidence.

Discussion of the clitoris is included here to anticipate difficulty a beginner may have because of similarity in size of the adult female clitoris and the juvenile male penis. The distinction can be made with certainty by remembering that the penis is always spiraled and originates on the left wall of the cloaca, whereas the clitoris is never spiraled and originates in the exact midline of the anterior wall.

OPENING OF OVIDUCT

Hochbaum (1942) states that the females in young waterfowl have an occluding membrane across the opening where the functional left oviduct opens into the cloaca, but that this disappears when the reproductive system becomes mature. It thus serves to distinguish first-year birds from those that have gone through a breeding season. Asmundson, Gunn, and Klose (1937) have shown that in chickens this membrane is under specific control of the female sex hormone produced by the active ovary. It is not surprising, therefore, that the membrane is still intact in female Canada geese in their second year. They have lived through one breeding season but are still sexually inactive and the ovary has not secreted sufficient female sex hormone to bring about disappearance of the occluding membrane.

None of the pinioned geese in the flock at Bright Land Farm nested in their first or second years and only 25 per cent in their third year. When third-year geese were examined during the winter, some females (undoubtedly

birds that had nested) had no occluding membrane, while in others the membrane was intact. All geese in their fourth and subsequent years were paired and had nested.

Observation of the oviducal opening in live geese is more difficult than in live ducks. As Hochbaum (1942) suggested, an anesthetic was used to relax the cloaca. Metycaine[4] is one of the best local anesthetics (Sollmann, 1942, p. 325), and was made up in 10 per cent aqueous solution just prior to use. A pledget of cotton soaked in the solution is inserted into the cloaca with a tab sticking out to prevent its loss into the rectum. After 2 to 3 minutes the cotton is removed and a pair of well-rounded forceps inserted into the cloaca and allowed to open, spreading the cloacal lips. A blunt smooth instrument must be used to probe the left cloacal wall in search of the sphincter muscle surrounding and marking the opening of the oviduct. The opening is usually collapsed, appearing as a mere slit.

BURSA OF FABRICIUS

Hochbaum (1942) and Hawkins were aware that the cloacal characters of immaturity persist in some or all Canada geese during the second year. This feature was studied in live geese at Bright Land Farm and with dead geese in hunters' bags at Horse Shoe Lake.

To measure depth of the bursa, a gauge (Fig. 5, below) was made from two secondary feathers of geese and a celluloid rule. The quill of one feather was cut across about 12 mm. below the vane, and the basal portion cleaned out with pointed forceps. A strip was cut from the rule, to provide the markings up to 45 mm., and this was inserted in the basal portion of the feather quill. The other secondary was then inserted into the open end of the cut shaft, thus holding the celluloid strip firmly against one side; this greatly increased its visibility and also provided a firm but flexible handle. The junction was closed with Scotch tape. The advantage of this instrument as compared with the glass gauge described by Kirkpatrick (1944) is in ease of construction, flexibility, and durability.

To measure the bursa in live geese requires the help and anesthetic mentioned above under "Oviduct Opening." For inspecting the bursa in dead geese, the anterior lip of the cloaca is cut, as described above, and the bursa depth gauge pushed gently along the posterior dorsal wall of the cloaca. Skill is soon acquired in placing the instrument in the proper opening, and not pushing through the distal part of the bursa to eliminate the end point. Care should also be taken that the forward lip of the bursa is clearly seen against the shaft of the inserted instrument so that the reading will be the actual depth of the bursa and not include that of the cloaca.

Measuring the bursal depth in a limited number of live geese of known age at Bright Land Farm during January showed a bursa 10 to 23 mm. deep in second year birds; in birds a year older (third year of life) the bursa was usually present and up to 15 mm.

[4] Hochbaum (1942) used cocaine, but metycaine seems more convenient, being stable to heat, light, and air. It is not a habit forming drug and therefore is more readily obtainable.

in depth. In others of the latter age group the bursa was resorbed so that only a crescentic slit 1 to 3 mm. in depth remained. Kirkpatrick (1944), working with pheasants, rightfully considered such bursas as closed. These older geese had open oviducts, indicating that they had bred. In all older geese (fourth or subsequent years) the bursa was completely resorbed.

the depth of bursa distribution was as follows:

0– 6 mm.	9
7–12	3
13–18	7
19–24	6
25–30	8
31–36	4
37–42	2

These figures indicate that the bursa

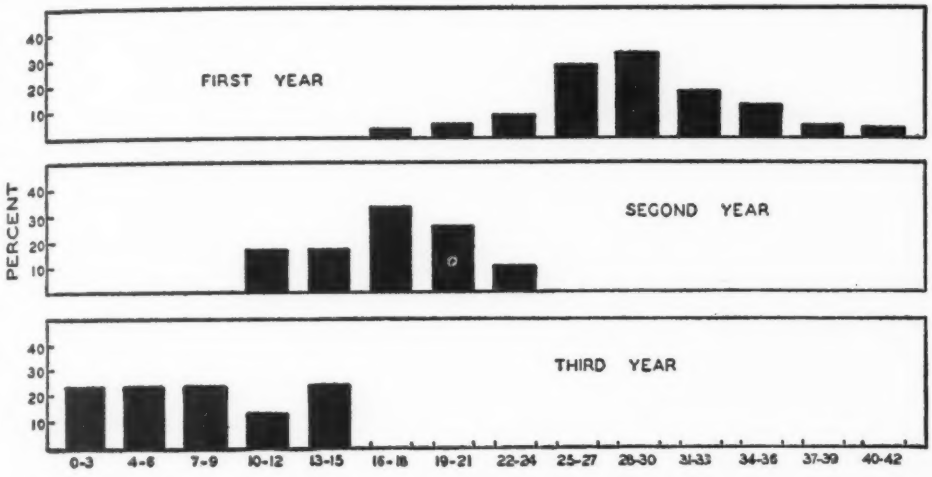


Fig. 6. Depth of bursa of Fabricius (in millimeters) in 264 Canada geese. First-year group, 243 from hunters' bags; second-year group, 12 live birds at Bright Land Farm; third-year group, 9 live geese at Bright Land Farm.

Figure 6 gives the distribution of measurements for the bursa in 243 first year geese—as indicated by their having notched tail feathers. This large sample was from geese shot by hunters at Horse Shoe Lake. Wild birds in their first winter have bursas from those of maximum size (42 mm.) to those more than 50 per cent resorbed (16 mm.). There was no difference between the sexes. Of birds more than one year of age (without notched tail feathers) examined in hunters' bags, of some wild geese may not start to regress until toward the end of the second year. Had the sample of second-year birds from Bright Land Farm been larger, the same distribution probably would have been found; but semi-domestic birds may mature more rapidly than those in the wild.

On the basis of this evidence, geese without a bursa are three or more years old; those with the bursa less than 15 mm. deep are in their second or third year; geese possessing a bursa of more

than 15 mm. in depth may be in the first, second, or third year. Asmundson, Gunn, and Klose (1937) have shown that regression of the bursa in chickens is under influence of sex hormones, and Kirkpatrick (1944) has found the same in pheasants; it seems, therefore, that the wide variation in rate of bursal regression in geese is further indication that they do not all reach breeding condition at the same age.

SUMMARY

1. Of 2,179 Canada geese weighed on their wintering ground at Horse Shoe Lake, Illinois, during October to March, only 6 exceeded 10 pounds in weight; all were males, and the largest weighed 11 pounds 9 ounces.

2. The weights of 1,028 live geese handled in banding studies were analyzed statistically. Juvenile females averaged 6.5 pounds, adult females 7.0 pounds, juvenile males 7.5 pounds, and adult males 8.4 pounds. There was a highly significant difference between the weights of juveniles and adults of both sexes, and between the weights of males and females at any age.

3. Comparison of November-December weights with those in January to March showed a significant loss in weight after close of the hunting season, when crops provided for geese on the Refuge were completely exhausted. The weight loss occurred as cold weather began, indicating that the carrying capacity of the Refuge had been exceeded and sporadic winter feeding was inadequate. This condition may affect the fecundity of adults and may also determine whether a young goose starts to breed in its second, third, or fourth year.

4. The simplest and most reliable criterion for distinguishing first-year geese is the notch in the tips of the tail feathers. The dull brown of these tail feathers and the flight feathers is in sharp contrast with the glossy black of those feathers on older birds. This criterion is especially useful for birds in which the tail molt has progressed so far that no clearly notched tail feathers remain. Notches are frequently lacking in the outer one to five pairs of rectrices.

5. The tail molt is continuous and centrifugal through the winter, but some juvenile birds leave on their northward migration without having acquired any adult tail feathers. A few adults were found in which the tail molt was being completed during the winter.

6. In all age and sex groups the number of tail feathers (rectrices) ranged from 14 to 19; juveniles had the maximum number as frequently as did adults. Of all geese examined, 86 per cent had 16 to 18 tail feathers.

7. Eight other types of plumage variation were examined as possible criteria of age and sex but most of them were either too infrequent, or present in all age and sex groups. White areas under the wings are limited to birds more than one year of age and present in one-third of this group.

8. Methods were devised for cloacal examination in both live and dead geese and instruments constructed to facilitate this and to measure bursal depth.

9. The size of the naked area surrounding the vent and the degree of pigmentation of that area and associated cloacal structures both increase with age, but the individual variation indicates these are criteria of physiological and not chronological age.

10. The penis of the juvenile male goose does not exceed 3×10 mm. in size and is an absolutely reliable age criterion. All older males have a much longer penis, and the basal sheath fills most of the left half of the cloaca. Some second year birds have a penis of intermediate size and in others it is of the same size as that of older geese and may show the bluish-black pigmentation of old ganders. This cannot be used widely as an age criterion.

11. In female geese there is a clitoris which apparently is homologous with the penis; but it is never spiraled like the male organ. It increases in length and pigmentation in older birds.

12. The opening of the oviduct into the cloaca is not evident until sexual maturity is reached. It was never found in second-year birds, but was open in some third-year birds in a captive flock.

13. Measurements of the bursa of Fabricius indicate much variability in the rate of its resorption in Canada geese. Resorption is incomplete during the first year and frequently even during the second year. Geese with no bursa are 3 or more years of age; those with a bursa less than 15 mm. in depth are 2 or 3 years of age; and geese with a bursa more than 15 mm. in depth may be in the first, second or third (?) year of life.

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BOBWHITE QUAIL REPRODUCTION IN SOUTHWESTERN TEXAS[1]

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The King Ranch, Kingsville, Texas

In southwestern Texas, populations of bobwhite (*Colinus virginianus*) usually fluctuate markedly from year to year. A pasture supporting one bird per two or three acres in spring may have a low population the following autumn. Conversely, a ranch where quail are scarce one year often supports many the following season.

Texas bobwhites may be more mobile than their relatives in the Southeast and the Mid-west, and fluctuations sometimes appear to result from ingress or egress stimulated by habitat change. Weather during the breeding season, and predation, also are important, as suggested by studies during the 1942 and 1943 breeding seasons. These studies embraced 194 nests on the W. W. Jones Wildlife Refuge in Jim Hogg County, Texas. All were situated in sandy mesquite semi-prairie grassland (Pl. 8, A, B), and most of them on or near a sample tract of 960 acres. The nests were located by use of a flushing bar mounted on a pick-up truck (Pl. 9, A); see also Lehmann and Davis, 1942; Lehmann, 1943).

Each nest was flagged by a small piece of cloth tied high in the top of the nearest mesquite, sometimes also by a mesquite stick driven into the ground 10 to 20 yards away. Nests were inspected at intervals of three to 10 days; on hot windy days they were always visited before noon when scent might be dispelled rapidly. Since automobile tracks were abundant over the ranch, investigators drove to within 50 yards

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of a nest at checking time and covered the remaining distance on foot or on stilts. Care was exercised to avoid attracting predators to nest sites, but such precautions may not always have been successful. The work did not materially increase nest losses, as was established by frequent population surveys on check areas in the same type of range.

Wherever possible, predators were identified by remains of egg shells, tracks, scats, and other sign at nests. The open character of the ground cover and the sandy soil facilitated the accumulation of evidence. All of the evidence was circumstantial and the possibility of errors in interpretation is admitted, but these probably were so few that they did not materially affect the conclusions.

NESTING SEASON

In 1942, pairs were observed as early as March 28, becoming common by April 6. In 1943 mating also occurred in late March and on April 13 the pairs outnumbered coveys 3 to 1. Covey disintegration was complete by the last week of April in both years.

Pairing was orderly, and most of the birds (evidenced from field observation and banding) selected mates from among members of their late spring groups. Persistent whistling, an indication of the presence of unmated cocks (Stoddard, 1931), was conspicuously absent. Pairs did not leave coveys immediately after mating; mated pairs and unmated covey remnants maintained loose associations for weeks. They often fed and roosted together, but pairs usually loafed apart from coveys and fighting resulted when they were driven together in trapping. The reproductive organs of females collected from such groups showed that laying sometimes began before covey bonds were broken. In fact, many hens apparently did not break off from their coveys until incubation began.

In 1942, no nests were found prior to the development of the nest-finding rig in early August. Laying in April and early May and the cessation of breeding during the peak of a drought (mid-May–June 25) were proved by autopsies. Rains June 26–July 5 stimulated laying; 24 partly or entirely successful nests began during the following periods:

July 1–July 10	3	July 21–July 30	6
July 11–July 20	9	July 31–Aug. 8	6

Of these, 17 (over 70%) hatched from August 9 through August 31 and 7 in the first week in September. Autumn trapping indicated the period from about August 10 through September 10 as the peak of hatching in 1942, but one brood trapped in October hatched about September 30. The 1942 breeding season, therefore, began in late March and extended through September.

In 1943, 64 nests yielded acceptable data on laying dates; one began about April 11, and one or more others each week from April 18 through August 8 except for an interval of 20 days from June 25 to July 15. The approximate hatching dates are presented in Table 1. Autumn trapping revealed a few young hatched as late as September 25. Breeding thus was spread over about 200 days from late March through September as in 1942.

NEST LOCATIONS AND COVER

Rather open mesquite semi-prairie

was the most popular nesting range. Woody plants were important only as shade and as whistling posts; only two of 194 nests were immediately beneath woody plants, a cactus (*Opuntia lindheimeri*) and a catclaw (*Acacia*). Forty-two nests were within 10 yards of roads

TABLE 1.—HATCHING DATES FOR BOBWHITE QUAIL NESTS, JIM HOGG COUNTY, TEXAS, 1943.

	Number of nests
June 1–10	9
11–20	3
21–30	1
July 1–10	7
11–20	15
21–31	4
Aug. 1–10	1
11–20	4
21–31	6
Sept. 1–10	9

or trails; the naturally wide spacing of South Texas plants provided an abundance of open spots and travelways elsewhere.

Interesting and perhaps significant was the fact that many early spring nests were grouped around covey headquarters areas of the preceding autumn and winter. In 1943, for example, five were found within 150 yards of Territory 218, and seven within the same distance of Territory 219. After early nesting efforts fared badly because of heavy coyote predation (10 of 12 nests destroyed), most of the pairs moved. Intensive periodic search with the nest-finding rig revealed only two nests in Territories 218 and 219 during the remainder of the breeding season.

On large land ownerships, summer movement influenced by predation would be of little importance, but if the tendency to drift after early nest loss is general, predator control might be of considerable importance in management on small tracts.

NESTING COVER

Six genera of grasses (*Andropogon, Aristida, Manisuris, Paspalum, Panicum*, and *Eragrostis*) were used as nesting cover. Only bluestem or sage grass (*Andropogon*), needle grass (*Aristida*), and joint grass (*Manisuris*) were important; they were the principal materials in 189 nests, or 97.5 per cent of those studied.

Bluestem (Pl. 8, C) was the exclusive outside covering of 76 nests (39%). Needle grass predominated in 59 (31%) and joint grass in 38 (19%). As is indicated in Table 2, bluestem was most popular in two periods, the late summer of 1942 and the spring of 1943. Popularity at these seasons resulted from the great durability of that grass; it weathered drought in the early summer of 1942 and in the winter of 1942–43 better than other species. In addition to providing good season-long nesting cover, bluestem demonstrated especially desirable emergency qualities. In fact, it is an indicator species in evaluating nesting conditions on southwestern Texas ranges.

HEIGHT OF GRASS

In 1942 the maximum height of clumps of grass concealing 52 quail nests averaged 25 (12 to 40) inches (Pl. 8, F), and in 1943, gross height averaged 23.7 (8 to 40) inches. Most of the blades in each clump—those of greatest importance in concealing nests—were 8 to 20 inches tall in 1942 and 5 to 9 inches in 1943, with averages of 12 and 9.2 inches, respectively. The gross and average heights did not vary appreciably from spring through late summer 1943, being as follows: May,

22.9–9.2; July, 24.7–8.9; and August, 23.5–9.7. Evidently local bobwhites prefer clumps of grass about 9 inches tall for nesting. Favorable nesting conditions can best be maintained through moderate grazing.

GREEN GRASS MATERIAL

The percentage of green blades in clumps of grass sheltering quail nests averaged 60 (15 to 90) per cent at the discovery dates of 52 nests in 1942, and 40 (10 to 90) per cent in 1943. Nest linings, on the other hand, were amost exclusively of dry or dead grass.

The ratio of green to dry grass in the outside of nest structures changed as incubation progressed. Bobwhites seemed to prefer to locate nests in clumps of grass containing considerable green material, possibly because they were cooler than dry grass.

The general "cast" of the ground cover was an accurate barometer of laying activity; when predominately green the bobwhites nested, but when it had a brownish or "parched" cast, laying was largely postponed until rain brought improvement.

NEST INTERIORS

In 1942, the nest bowls, at the top, measured 4.4 (3.5–6.75) inches in diameter, and 4 (3.25 to 6) inches in 1943. The unusual feature was their great depth: 3 (2.5 to 4) inches in 1942, and 2.7 inches in 1943. When birds were incubating, the tops of their backs were usually level with or only slightly above the surface of the ground, and their heads were barely above ground level. Deep nest bowls gave protection against the summer heat, remaining quite cool when the soil surface nearby was hot; but no tendency was noticed to deepen nest bowls as the weather warmed.

TABLE 2.—NUMBERS OF BOBWHITE QUAIL NESTS CONCEALED IN VARIOUS KINDS OF GRASSES, JIM HOGG COUNTY, TEXAS.

	Spring 1943	Mid-summer 1943	Late summer 1943	Late summer 1942	Totals
Bluestem	23	16	9	28	76
Needle	12	20	14	13	59
Joint	7	10	14	7	38
Paspalum	1	0	0	0	1
Panic	0	0	0	3	3
Love	0	0	0	1	1
Bluestem-needle	2	3	1	0	6
Bluestem-joint	0	1	0	0	1
Joint-needle	1	0	2	0	3
Joint-panic	2	0	0	0	2
Needle-panic	2	1	0	0	3
Paspalum-needle	1	0	0	0	1
Totals	51	51	40	52	194

ROOFING

In the 1942 series of 52 nests, 39 (75%) were well roofed in that the eggs were invisible from above, and in 1943 107 (almost 75%) were so covered. Roofing was evaluated as fairly good (eggs barely noticeable) in 28 nests (20%),

and seven (5%) had poor cover in 1943; 11 (21%) were fairly well roofed, and two (4%) poorly covered in 1944. Nests were roofed principally by the natural intertwining of the blades of grass. In some cases the roofing was deliberately strengthened (Pl. 8, G) possibly by the birds; 19 of that type were found in 1942, and 16 in 1943.

ENTRANCES

Seven nests were so well concealed that the entrances were not apparent, and two others might have been entered from several directions. Of the remaining 177, 76 faced west, 52 south, 35 north, and 14 to the east or southeast. It may have been more than a coincidence that 43 per cent of the nests faced west and only about 8 per cent to the east and southeast into the prevailing winds.

CONCEALMENT

By arbitrary standards which considered the visibility of eggs at a distance of 5 feet above and from all sides of a nest, 22 (42%) were excellently hidden, 14 (27%) were well hidden, 14 (27%) fairly well hidden, and only 3 (4%) poorly concealed in 1942. Of 142 nests studied in 1943, 40 (28%) were excellently hidden, 63 (44%) well hidden, 32 (23%) fairly well hidden, and 7 (5%) were poorly concealed. Heavy ground cover was available within a few feet of each poorly concealed nest; birds could have used it had they desired. It appeared, therefore, that some pairs simply preferred lighter nesting cover than others (Pl. 8, H), just as some coveys occupy winter ranges where woody growth is decidedly below what might be considered the "mean" for the species. The present studies did not support Stoddard's conclusion (1931, p. 25) that birds tolerate exposed nesting sites rather than leave favorite range. Many instances were observed where heavy nesting populations dispersed under heavy grazing pressure. The bulk of the nests studied were well hidden, and heavy predation on those nests could scarcely be attributed to inferior cover.

Largely because of the sandy character of the soil, all nests were located where flooding was unlikely, even during heavy rains.

EGG CLUTCHES AND INCUBATION

In 1943, 48 complete spring clutches contained 7 to 24 eggs and averaged 14.8; in mid-summer 47 had 8 to 18 eggs, averaging 11.4; and in late summer, 40 clutches averaged only 10.5. In the late summer of the previous year, the average size of 52 clutches was 10.9 eggs and two pairs of quail set on only 5 eggs each. The average size of the clutches decreased, therefore, as the nesting season advanced.

In spring, the hatchability was high; of 231 eggs in 15 nests in May and early June of 1943, 217 (94%) hatched. Ten others contained advanced embryos, most of which were alive inside the shells when examined by the investigators. Only four eggs were infertile.

In the mid-summer (July) series of 31 nests containing 371 eggs unmolested by egg-eating predators, hatchability was lower. Chicks were realized from only 296 eggs (about 80%); 53 eggs (about 14%) were infertile, and 9 embryos died early in incubation. Four chicks were advanced and alive, but too weak to pip the shells. Nine partially hatched young were killed by fire ants

(*Solenopsis*); these insects were not nest predators earlier in the year.

In late summer, the percentage hatch was further reduced; only 162 of 229 eggs (71%) in 22 nests produced chicks; 46 eggs (20%) were infertile, and 3 contained dead embryos. Eighteen, or twice as many as in midsummer, were destroyed by fire ants. Thus, a successful nest in spring produced about 14 chicks, but about 7 in late summer.

Data on the size of spring clutches (14.8) as compared with those of midsummer (11.4) and late summer (10.5 to 10.9), together with the greater percentage hatch in spring (94%) as compared to mid-summer (80%) and late summer (71%), are potent arguments in favor of management to save larger numbers of spring nests. Granting that all pairs whose efforts in spring were unsuccessful later renested and brought off broods before the summer was over, the annual production would have been about doubled if early nests had been successful. Ample range to accommodate increase was available, for the Jones Wildlife Refuge as a whole (165,000 acres) and the surrounding territory were underpopulated.

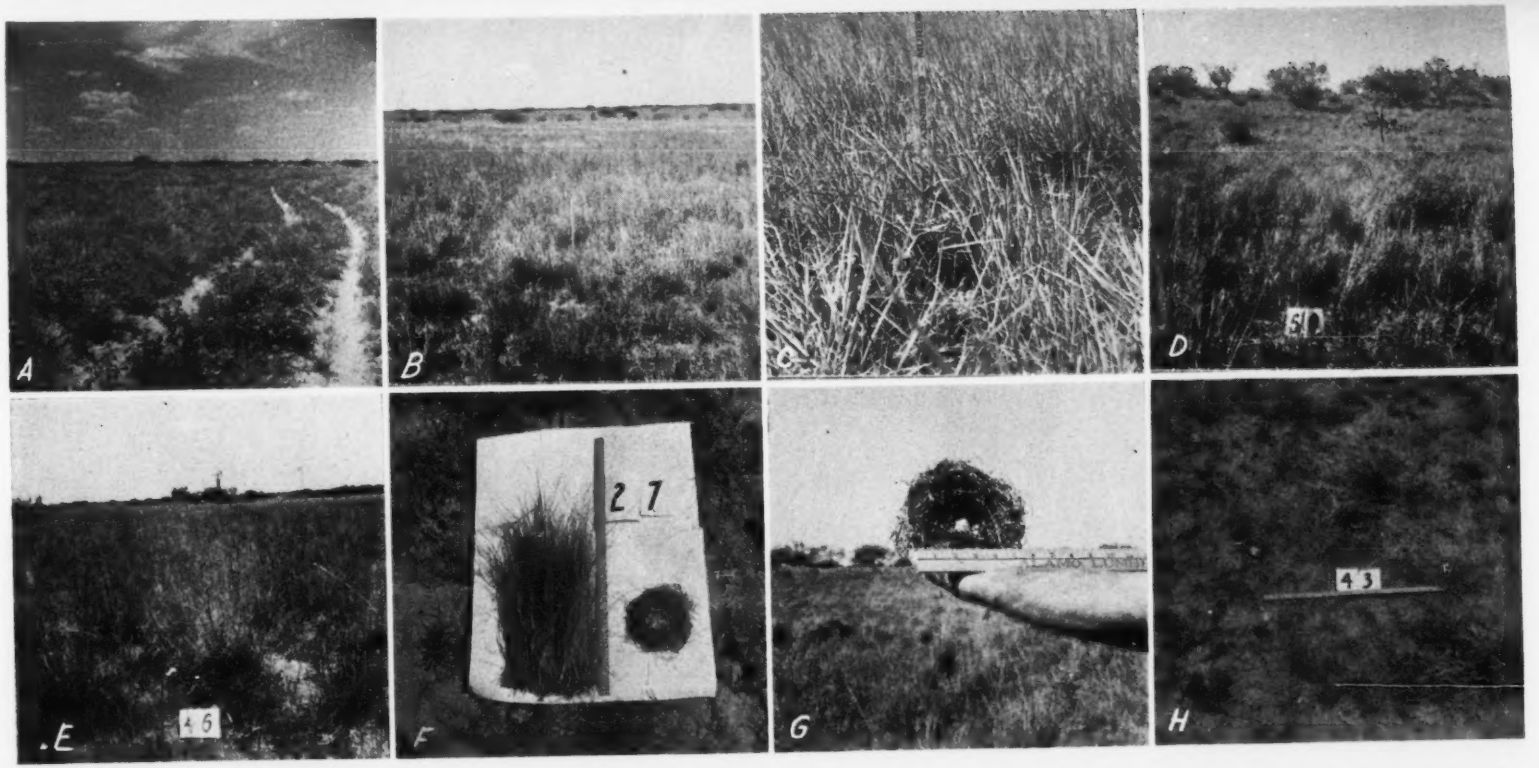
In 1942, males incubated three nests, females 45, and both sexes three. In the latter instances, hens were setting when the nests were found but males took over before they were terminated. If the hens were killed, no sign was evident near the nests. In 1943, hens incubated 133 nests, males five, and both sexes covered four. No instance was found of the sexes alternating in incubation, or of hens relieving males.

Stoddard (1931, p. 32) found that incubating bobwhites normally left their nests for feeding and recreation once each day, usually in the afternoon. The Texas birds usually left their nests twice a day, in early morning and in late afternoon. Morning feeding was sometimes dispensed with when hatching was near, however, and the quail never left their nests, unless disturbed, when hatching was in progress. During incubation, the birds usually left their nests at the first sign of a shower, possibly because it was advantageous for the eggs to soak up moisture.

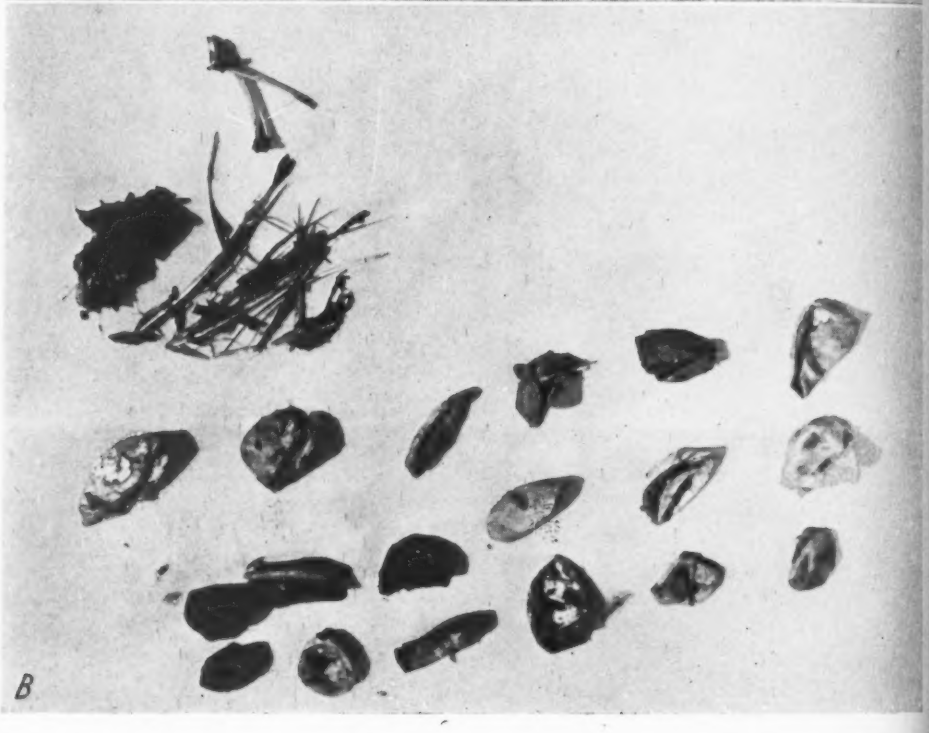
TABLE 3.—SUMMARY OF RESULTS IN 189 NESTS OF BOBWHITE QUAIL IN TEXAS.[a]

Terminated by	Late summer 1942		Spring 1943		Mid-summer 1943		Late summer 1943		Totals	
	Number	Percentage	Number	Percentage	Number	Percentage	Number	Percentage	Number	Percentage
Hatching[b]	25	*49*	15	*30*	28	*57*	19	*49*	87	*46*
Coyote	26	*51*	29	*58*	12	*25*	13	*33*	80	*43*
Skunk	0	—	6	*12*	4	*8*	4	*10*	14	*7*
Snake	0	—	0	—	2	*4*	0	—	2	*1*
Desertion[c]	0	—	0	—	3	6	3	*8*	6	*3*
Total	51	—	50	—	49	—	39	—	189	—

[a] Five nests in which one or more eggs were broken by nest-finding rig were omitted.
[b] All or in part.
[c] All eggs in 5 nests infertile.



Nesting cover of bobwhite quail, W. W. Jones Wildlife Refuge, Jim Hogg County, Texas. Photographs by V. W. Lehmann. *A*, *B*. Sandy mesquite semi-prairie where nests were located. *C*. Nest well concealed in bluestem or sage grass. *D*. Nest concealed mainly by needle grass (*Aristida*). *E*. Nest in joint grass (*Manisuris*), a type of cover much used in late summer. *F*. Bluestem grass used both for concealment and lining. *G*. Nest lining with well constructed roof. *H*. Poorly concealed nest in needle grass; heavy bluestem cover was available within 25 yards.



A. Wide flushing bar mounted on front bumper of pick-up truck and used to locate nests of bobwhite quail in flat open country. *B*. Contents of a coyote stomach, May 1943. Bones and feathers of adult quail (upper left) and remains of egg shells. W. W. Jones Wildlife Refuge, Jim Hogg County, Texas. Photographs by V. W. Lehmann.

FATE OF NESTS

The results of 189 nesting efforts are summarized in Table 3. In 1943, 15 nests (30%) in spring, 28 (57%) in mid-summer, and 19 (49%) in late summer hatched entirely or in part. In the late summer of 1942, 25 of 51 nests (49%) succeeded all or partially. A total of 87 (about 46%) of the study nests were successful.

Six nests (4%) were deserted. All were abandoned during especially hot weather, probably because of excessive heat. When shade temperatures soared above 105 F. it appeared that quail simply could not incubate in exposed situations.

Ninety-six nests, about half of those studied, were destroyed by predators; losses were attributed to coyotes, skunks, and snakes. Skunks took 14 nests and accounted for approximately 15 per cent of all predation; the striped skunk (*Mephitis mephitis varians*) probably accomplished most of the damage since the hog-nosed skunk (*Conepatus leuconotus texensis*) and the spotted skunk (*Spilogale leucoparia*) were rare. Skunk predation did not vary more than 4 per cent per series of nests followed, and, unlike coyote damage, it was not especially high in early spring. Damage by skunks and by coyotes was not intercompensatory; i.e., skunk damage did not increase as coyote pressure decreased in mid-summer. "White racers" (probably *Coluber* or *Masticophis*) may have taken both nests attributed to snakes since they were fairly common on the study area, whereas other reptiles were rare. Fire ants killed 38 partly or completely hatched young in 12 nests, but they did not destroy any clutches completely. The coyote (*Canis latrans*) proved to be the outstandingly destructive agency, accounting for 80 nests and about 83 per cent of all predation.

COYOTE PREDATION

There was heavy coyote predation on early nests, fifty per cent of this being from late April through early June 1943. Some of the circumstances surrounding that loss are known. Quail concentrated for nesting in open country, possibly because grassy nesting cover was best in areas where mesquite and other woody plants were scarce. Coyotes also preferred open country in spring and early summer. Open sandy knolls provided choice den sites for rearing pups. Grasshoppers, jack rabbits, and quail-eggs—all of them important coyote foods on the study area—were more numerous there than in brushy territory. The stomachs of 14 coyotes collected from May 21 to June 15, 1943, near one study area contained the following: quail eggs and quail, 37%; small mammals (mostly jack rabbit), 34%; insects (mostly grasshoppers), 14%; and vegetable products (early maturing mesquite beans and prickly pear tunas), 1%. Quail eggs (9 to 26) were found in 9 stomachs (Pl. 9, B); and flesh of Hereford calves in four. At least one calf appeared to represent a fresh kill.

In mid-summer, coyote damage to nesting quail was relatively light. From June 20 to August 10, 1943, coyotes took only 25 per cent of the study nests as compared to 58 per cent during the preceding six weeks. Nesting activity was brisk in this period of lessened predation. The nesting cover was scarcely improved, but a buffer food supply of vegetable foods had reached

a seasonal high in brushy range. Heavy "mast" crops of mesquite beans (*Prosopis*), prickly pear tunas (*Opuntia lindheimeri*), Mexican persimmons (*Diospyros texana*), and granjeno berries (*Celtis pallida*) ripened in quantity during late June of both years. The coyotes then shifted their activities from the prairies to the brushland and changed their diet as well. Vegetable foods comprised only one per cent of the contents of 14 coyote stomachs collected prior to June 15, but made up 29 per cent in 25 stomachs taken between June 16 and June 25.

The coyotes were largely vegetarians so long as the mast crop held out. Late summer rains hastened its decline, however, and grasshoppers and quail nests increased on the prairie. As vegetable foods decreased, losses in quail nests increased in both 1942 and 1943. Coyotes accounted for half of a series of 51 study nests from mid-August through mid-September in 1942, and one third of 39 nests in the late summer of 1943. The somewhat lower loss late in the summer of 1943 may have resulted from intensive coyote trapping from May to July in the pasture where many study nests were located.

Coyote predation was not always proportional to nesting activity; nesting was heavy each July, but losses in study nests were relatively light in that month. Nor was pressure appreciably heavier in pastures or parts of pastures where nest density was greatest. One series of 26 nests studied during the summer of 1943 suffered a 27 per cent loss to coyotes and another series of 24 lost 25 per cent. Data compiled through use of the nest-finding rig revealed that active nests were about five times as numerous in the one area as in the other, whereas mortality was only two per cent higher.

The degree of nest concealment, according to human standards, was of little importance in regulating nesting success at any season; coyote pressure was as heavy on nests excellently hidden as on those only fairly well concealed. Mortality among the incubating birds was not positively correlated with nest construction; all except one of the 14 parent birds killed at study nests in two breeding seasons were incubating on nests that were well constructed and well concealed. Evidently these losses resulted because the birds could not make rapid exits through the tops or sides of such nests, but only through the entrances.

Cover in pastures or parts of pastures containing study nests varied in height and density from rather light to very heavy, but coyotes appeared as adept at locating nests in heavy cover as in light growth. It could not be established that good ground cover was an adequate

TABLE 4.—AGE AND SEX RATIOS IN AUTUMN POPULATIONS OF BOBWHITE QUAIL, JIM HOGG COUNTY, TEXAS.

Year	Number trapped	Adults		Total adults	Young			Total young	Age unknown
		Males	Females		Male	Female	?		
1942	549	105	48	153	164	196	29	389	7
1943	576	166	123	289	135	127	16	278	9

safeguard against heavy loss. Nesting during mid-summer when the bulk of the coyote population was enjoying the highly palatable produce of brushy range, in fact, appeared the best insurance against coyote destruction.

POPULATION INCREASE

On the 960-acre study area, the quail population increased from 378 in April 1942, to 596 in the autumn of 1942. In 1943 the numbers rose from 619 in late winter (1942–43), to 735 in the autumn of that year. The rate of population increase, therefore, was about 58 per cent in 1942, and 18 per cent in 1943.

The composition of autumn populations, as revealed by trapping, are persented in Table 4. The total number of young trapped on the area was greater in 1942 (389) than in 1943 (278). There were about 2.5 young to each adult in 1942, but adults outnumbered young at the time the check was made in 1943. Both breeding seasons, therefore, were successful in that some young were produced and the population density increased. The data suggest, however, that the 1942 breeding season, from the standpoint of young compared to adults, was more successful than that of 1943; such, however, was scarcely the case. The population data, complete as they are, merely serve to indicate that censuses and age classifications in autumn are poor indices of breeding success on a small area; their use without supplementary data on such matters as type of habitat, population levels as related to carrying capacity, egress, etc., may lead to conclusions of questionable accuracy (Errington, 1942).

Insofar as the winter carrying capacity of an area for quail is concerned, one must not forget that habitats sometimes fluctuate much in the same manner as do populations. From the standpoint of habitat, quail ranges in Texas are of two distinct types, "flexible" and "static," with varying degrees of intergradation. The outstanding characteristic of flexible range is the ability of the food and cover to accommodate many more coveys in some years than in others. Vast areas of the Texas Panhandle and the Southwestern grazing land are of this type. Scanty herbaceous growth and woody cover, usually mesquite, too "open" for quail are usual habitat deficiencies. When the rainfall is generous and opportune, however, rough grasses and weeds largely unpalatable to livestock are produced in quantity; such luxuriant ground cover compensates to a degree for scanty woody growth. Woody cover is also improved directly; however, tall grass and weeds under low branching mesquites transform cover ordinarily too open into good headquarters sites. The larger quail crops of "wet" years, therefore, often find habitats improved to accommodate them. In such instances, autumn and winter populations may accurately reflect the success of reproduction.

On typically static quail range, one or several habitat factors which are limiting, remain relatively constant from one winter to the next. Often the limiting factor is woody cover; usually it is deficient in amount rather than quality. In the Bernard Prairie of Colorado County, for example, all of the woody cover in a large pasture may consist of a half dozen rose hedges; a farm in Washington County may have only two disjunct blocks of woody cover, a

tangle of vines at the head of a gully and a clump of yaupon (*Ilex vomitoria*) on the edge of a meadow. In either area the woody cover is of high quality regardless of whether the growing season is good or poor. Quail reproduction and food are vastly better in certain years than in others, but good years do not increase the quantity of woody cover. With few or no new ranges, young in numbers exceeding cover accommodations will disappear. For that reason, censuses of autumn or winter populations do not measure reproduction accurately except, perhaps, when ranges are distinctly underpopulated.

Many young produced on an area may scatter before autumn. On our 960-acre study tract, egress was apparent by midsummer, stimulated by competition for dense shade. Mesquite trees were fairly numerous, and single birds and pairs sought relief from the intense mid-day heat in the shadows produced by the trunks and larger branches. Broods preferred more spacious accommodations, however, and sought clumps of tasajillo (*Opuntia leptocaulis*) and granjeno. These shrubs were relatively scarce on the tract; most of them were occupied by late June and all were in use by mid-July. When new broods hatched near choice loafing sites competition often resulted. At 17 such bushes, where frequent observations were made, 15 "old" broods vacated shortly after "new" broods appeared; combinations were effected in only two instances. Mixing was common on this heavily populated range, but seldom until junior members were beyond the chick stage. Possibly this was because the maternal instincts of adults were strongest at time of hatching, and diminished with time. Competition for shade is known to have resulted in more than minor territorial adjustments. Only six of 46 young banded near the geographic center of the study area on July 28, 1943, were recovered during extensive trapping the following autumn.

Of 278 young quail trapped on the area in October and November, 1943, only 76 were of those hatched in late spring and early summer. Study nests alone produced 217 young in 15 broods during this period. Of the trapped birds, 160 were hatched in mid-summer; study nests produced 192 young (18 broods) at that time. Thirty one birds of the fall catch were late summer chicks; the age class of 11 others was not recorded. Late study nests on the area produced 112 young in 11 broods. Study nests alone, which certainly included only a fraction of all the quail nests on the 960 acres, produced 521 chicks, or almost twice as many young as were trapped the following autumn.

Some young, of course, died before autumn trapping began. Stomach examination proved that coyotes sometimes catch two or three chicks from a single brood. The coyotes, however, catch few young able to fly, and the net effect of coyote predation on young quail is probably small. Other predators on young quail were conspicuous by their absence. There was no indication of heavy loss from disease; young were collected and examined for both internal and external parasites throughout the breeding season. Since it is known that juvenile mortality was not heavy, and because broods under frequent observation always disappeared *in toto*, it appears certain that a large

segment of the 1943 increase moved from the study area before autumn set in. The rate of annual increase on this area tended to be inverse to breeding density (Errington, 1942, p. 177); therefore it did not follow that breeding success also was inverse to population density. Conclusions concerning population recovery based largely on winter and spring censuses on specific tracts (Errington and Hamerstrom, 1936, p. 421–423), in fact, might be accepted as highly tentative until vastly more is known concerning summer spread.

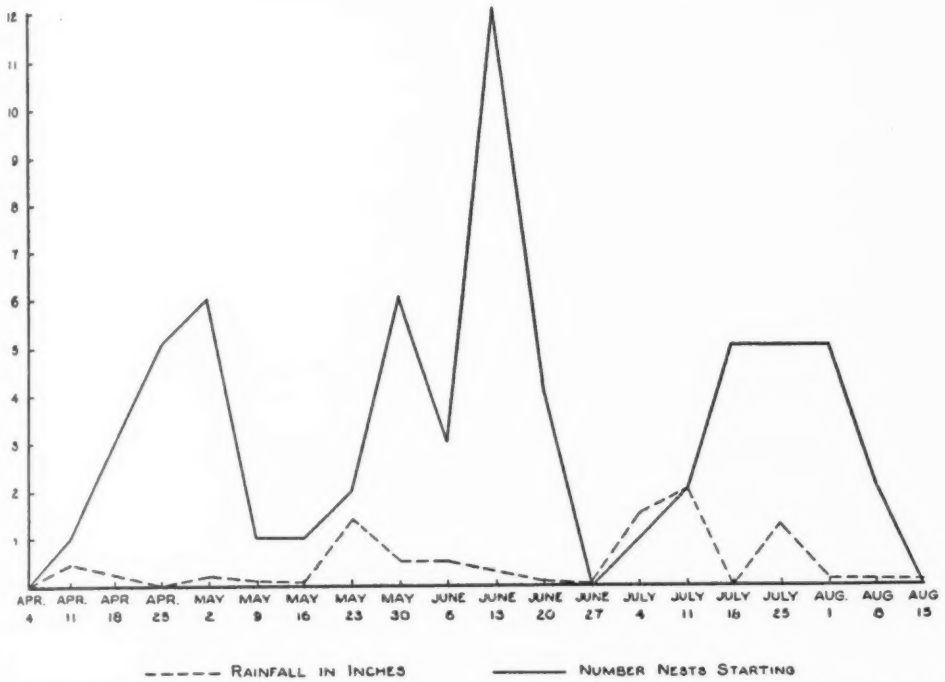


Fig. 1. Spring and summer rainfall in inches, by weeks, as related to laying activity of the bobwhite quail. W. W. Jones Wildlife Refuge, Jim Hogg County, Texas.

FACTORS REGULATING REPRODUCTION

In southwestern Texas, two factors appear outstandingly important in regulating bobwhite reproduction; weather and predation. Weather favorable to nesting may be anticipated each spring; quail lay when vegetation "greens out" from moisture stored during the winter rains. On uncontrolled range, however, predators (principally coyotes on our areas) destroy many if not most early nests; and renesting in southwestern Texas is not always rapid. In the absence of appreciable moisture (1.37 inches from March through June, 1942), quail on the Jones Wildlife Refuge congregated into non-breeding associations of 6 to 16; breeding was not resumed until the drought was broken in July. Rainfall, therefore, was important in stimulating renesting in 1942;

it was also important in 1943. Nesting activity soared following the rains of April 11, May 23, and July 4 to 11 (Fig. 1); these peak periods were actually more pronounced than the chart indicates because nest finding in each period was suspended after a predetermined number had been located. When there are rains to stimulate renesting in mid-summer, large numbers of young quail may be produced because coyote use of semi-prairie range is relatively slight in that season. In the absence of summer rains, which stimulate renesting and partly compensate for early losses, reproduction may be insignificant. One could hardly predict renesting periods in advance for Texas quail (Errington, 1942) unless it were possible to determine in advance when the rains would come.

On the basis of U. S. Weather Bureau records since 1914 at Hebbronville, Texas, it is apparent that rain in midsummer is not dependable and occurs only about one year in three. For sustained quail production, large crops of young are desired not one year in three but every year. While man cannot regulate the weather, he can control coyotes, and such control to reduce what now appears to be terrific pressure on spring and late summer nestings appears worthy of serious consideration as a management technique on otherwise suitable areas in southwestern Texas where annual shootable crops of quail are desired. It does not follow that coyotes should be entirely eliminated or that most areas could support heavy populations if coyotes were controlled. Improvement of deficient food and cover resulting from overgrazing is also important on many areas.

SUMMARY AND CONCLUSIONS

Studies involving 194 bobwhite nests on the W. W. Jones Wildlife Refuge, Jim Hogg County, Texas, in 1942 and 1943 revealed that breeding extended from late March through September. Pairing was principally among members of the same coveys, and laying sometimes began before covey bonds were broken. Breeding activity was staggered; renesting was influenced importantly by rainfall.

Mesquite semi-prairie was the most popular breeding range; many early nests were located within winter territories. Bluestem, joint grass, and needle grass were favorite nesting cover, being the principal covering for 97.5 per cent of all nests studied. Bluestem was especially important because of its resistance to drought and to the rigors of winter.

Quail evidently preferred to nest in grass about 9 inches tall containing considerable green material, possibly because green blades provided superior protection from summer heat. The general "cast" of ground cover proved an accurate barometer of laying activity which was appreciable only when ground cover was green.

Nest bowls averaged about 4 inches in diameter at the top and 2.5 inches in depth. Deep nest bowls afforded considerable protection from summer heat. About three-fourths of all nests were well roofed; most entrances faced away from prevailing winds. A majority of the nests were well concealed according to human standards, and all were in well drained situations.

The average size of egg clutch decreased as the nesting season progressed; in the spring of 1943 they averaged 14.8 eggs, but only 10.5 in late

summer. Hatchability was high (about 94%) in spring, but decreased (71%) as the weather warmed. Successful renestings produced only about half as many chicks as spring layings.

Of 138 nests during 1943 that hatched all or in part, 15 were in spring (30%), 28 in midsummer (57%), and 19 in late summer (49%). Twenty-five of 51 hatched in the late summer of 1942. Thus 87 of 189 study nests (46%) succeeded. Six nests were deserted and predators terminated 96 (50%). Predator damage was by coyotes (80 nests, 83%), skunks (14 nests, 15%), and snakes (2 nests). Fire ants destroyed 38 eggs and young in 12 nests, but were not responsible for the complete loss of any clutch.

Coyote predation was not regular and sustained; peaks in spring and late summer and a "low" in mid-summer were recorded. The mid-summer low was correlated with the maturing of buffer vegetable foods in brushy territory. Coyote predation was not proportional to nesting activity; nest losses were not positively correlated with breeding density, cover conditions, or concealment of individual nests.

The bobwhite population on the 960-acre study area in autumn and winter were not accurate indices of breeding success. Quail ranges, as to winter carrying capacity, are of two major types: flexible and static. Flexible range can accommodate more coveys in certain years than in others, but "good" years produce few new territories in static range. Autumn and winter populations, therefore, are poor barometers of breeding success on static ranges unless the latter are decidedly underpopulated. The rate of increase tends to be inverse to breeding density on static range, but breeding success is not necessarily inverse to population density. In such areas, summer spread may siphon off much of the annual increase before autumn.

Important factors regulating quail reproduction in southwestern Texas are rainfall, through its effect on nesting activity, and coyote predation, because of its severity except in mid-summer. Coyote control might promote larger annual crops of young birds on many areas where food and cover appear adequate for heavier densities than under present conditions. Quail are limited by overgrazing on many ranches, however, and extensive coyote control on such areas would hardly be justified for quail increase.

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MOBILITY OF BOBWHITE QUAIL IN SOUTHWESTERN TEXAS[1]

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For many years the bobwhite quail (*Colinus virginianus*) has been considered a species of low mobility. Stoddard's banding studies in the Southeast (1931) suggested that many quail were relatively sedentary and Errington (1933) in Wisconsin reached the same conclusion. Leopold (1933) summarized the findings of these and other investigators as follows: "... nearly half the quail spend their life-span within a quarter mile of their birthplace, while few ever wander more than a mile. The covey range during fall or winter is often under 400 yards. Individuals rather than coveys are the unit of movement. The great bulk of movement occurred by the shifting of individuals as between coveys.

"Errington's more limited banding of quail in Wisconsin corroborates Stoddard's findings, but he found little movement of either individuals or coveys in midwinter, except under stress of starvation.

"In all probability the quail is the least mobile species of American game."

Some of our early studies in Texas also suggest that bobwhites often are quite sedentary (Lehmann, 1937a, 1937b), but later findings do not fully substantiate that conclusion. On three tracts of 1,723 acres in Walker County where H. R. Siegler, H. C. Hahn, Jr., and the writer conducted intensive studies in 1936–38 under the Texas Cooperative Wildlife Research Unit, quail density fluctuated to an extent unexplainable on the basis of habitat changes, weather, and predation. Of 142 banded in the early spring of 1936 only 6 were recovered in our traps, which took 132 of approximately 246 birds present the following autumn. Quail decreased to 130 on this project in the winter of 1937–38 despite superior habitat conditions and almost complete protection from shooting. On the study areas, therefore, either heavy predation occurred and escaped our attention on daily patrols, or many birds moved away. At least 6 individuals did move and were killed 3 to 9 (average 6.6) miles from the project.

Twenty returns were secured from 249 birds banded by H. R. Siegler, R. H. Baker, and the writer in northeastern Colorado County, Texas in 1938–40. Four remained in the same winter territories for as long as 12 months; the 16 others moved an average of 1.2 (0.25–10.5) miles. Certain winter territories were relatively permanent, but covey size and composition

[1] Texas Cooperative Wildlife Research Unit: U. S. Fish and Wildlife Service; Agricultural and Mechanical College of Texas; Texas Game Fish and Oyster Commission; and American Wildlife Institute, cooperating. Walter P. Taylor and William B. Davis gave editorial and other assistance; helpful aid was given by Mr. and Mrs. F. M. Lewis and Charlie Edwards of the Jones Ranch, Jim Hogg County, Texas. J. B. Davis assisted in field work from April 1942 to January 15, 1943, and W. G. Fuller from January 15, 1943, through April 1944.

varied greatly from season to season (Lehmann, 1940).

Fluctuations in population suggesting wholesale movement have been recorded on widely separated management areas in the State since 1938. In some cases, as on the Von Lengerke Ranch in Colorado County, Cinco Ranch in Harris County, and Hegar Farm in Harris County, the increase following habitat improvement was decidedly greater than the breeding potentials of the seed stock. On other areas, such as the Heist and White tracts in Dimmit County, large populations approaching a density of one bird per acre disappeared almost over night, despite superior food and cover conditions. Such fluctuations suggested the desirability of additional banding studies but intensive practical work required an efficient trap.

The standard quail trap developed by Stoddard (1931: 442–445) proved impractical under Texas conditions except for random sampling. Entire coveys were seldom caught and predation on the quail in traps was high. Use of buffer cloths reduced catches and removal of buffers resulted in extensive "scalping" of the birds. Rainy weather and good food conditions were serious handicaps; the traps were baited and baiting probably affected natural movement. A wire drive-type trap employing no bait otherwise vastly superior to other known types for work in semi-prairie country was developed by State Game Warden Herbert Ward of Catarina, Texas, about 1928 and improved by J. B. Davis and the writer in 1940–41 (Lehmann, 1941). The Ward Drive Trap was used to take the birds involved in this study (Pl. 10, B).

The study area was a tract of moderately grazed mesquite semi-prairie (Pl. 10, A) 1 x 1.5 miles, centered on the W. W. Jones Wildlife Refuge of 137,000 acres in Jim Hogg County. Ranch land of the same ecological type and closely patrolled to prevent poaching surrounded the study area and extended for 10 miles or more in all directions (except for a 1,000 acre shooting area on the adjoining Yeager Ranch, hunted each year). The woody cover was predominantly mesquite (*Prosopis*) and catclaw (*Acacia*), with a scattering of tasajillo (*Opuntia leptocaulis*), nopal (*Opuntia lindheimeri*), granjeno (*Celtis pallida*), and thorn bush (*Condalia*). Dominant grasses were needle grass (*Aristida*) and bluestem (*Andropogon*). Goatweed (*Croton*), perennial ragweed (*Ambrosia psilostachya*), and many other seed-bearing weeds were numerous; habitat conditions for quail apparently were excellent on both the study area and surrounding area throughout the investigation, which extended from April 1, 1942, to February 15, 1944.

A total of 1,659 quail were banded on the 960-acre tract in less than 2 years, and 850 others were marked in adjacent territory. This yielded 787 movement records for 699 birds. In addition, 194 nests were studied on the Jones Ranch, more than 500 predator stomachs (principally of coyotes) were examined, several hundred bobwhites were examined for internal parasites and food content, and large scale censuses and habitat improvement experiments were conducted. Our data on quail movement are interpreted in the light of these supplementary studies.

POPULATIONS AND NUMBERS BANDED

It was apparent early in our studies that the quail population of our study area did not possess qualities of stability to the degree which Errington and Hamerstrom (1936), Stoddard (1931), and Leopold (1933) attribute to bobwhites in other regions. Some birds did assemble in rather well knit coveys and settle in definite ranges in autumn. Others did not, however, and the population of the study area, considered as a unit, was continuously changing. The rate of change was not constant; it flared and subsided periodically for reasons unknown. Withal, the movement of quail to and from the study area might well be compared to the movement of water through a pool in the bed of a slow moving stream. Some water is almost always entering the pool and some is flowing out. What might be termed "normal" flow and normal water levels are periodically upset by showers on the watershed.

Close determination of total and average quail populations for a particular season, therefore, would have necessitated daily trapping. Investigations at that level of intensity would have disturbed the quail unduly and would have been impractical for other reasons. Census work, therefore, was confined to trapping periods. The data obtained in no sense represent total populations for any given season, but give valuable clues as to population trends. The numbers of birds found and trapped are summarized in Table 1.

From April 1942 through November 1943 the population density almost doubled. Habitat conditions were consistently good, the breeding seasons were favorable, and there was no hunting on the study area or in nearby territory during the period. In other words there was no apparent environmental influence sufficient to account for the observed fluctuation. The population of the study area did not exceed 735 birds at any time during the census periods, but banding showed that a minimum of 1,659 individuals used the area at one time or another during the two years.

TABLE 1.—BOBWHITE QUAIL POPULATION OF A 960-ACRE STUDY AREA IN TEXAS.

Period	Population	Density (acres per quail)	Number Trapped
April 10–20, 1942	378	2.54	115
Oct. 12–Nov. 21, 1942	596	1.61	549
Jan. 16–Feb. 19, 1943	619	1.55	540
July 28, 1943	—	—	51
Oct. 9–Nov. 20, 1943	735	1.30	576
Jan. 25–Feb. 8, 1944	392	2.45	254

MOVEMENTS OF INDIVIDUALS

The distance that a bird moved during a particular period (e.g. autumn) was determined by the air-line distance between the initial and last trapping sites as measured on a map. When movement is given from one season to another, the points involved in computations were those where birds were last taken in one season and first trapped in the following season. Thus, if a bird was trapped at Station 219 on April 15, 1942, retaken at Station 211 on April 20, and trapped a third time at Station 226 on October 10, its movement for the period spring to autumn, 1942, is stated as the distance between Stations 211

and 226. Our records, therefore, are not measures of true movement; in most instances they more nearly portray minimum movement.

Since the study area was completely surrounded by miles of "wild" ranch lands supporting heavy quail populations, the recovery of banded birds moving considerable distances was almost accidental. Our data on movements of quail, like those previously presented by other investigators, therefore, are open to the criticism that they are mainly a measure of the travels of "sedentary" birds. This criticism is valid, and our records are presented with this qualification.

SPRING TO AUTUMN

Six birds banded in April 1942 were retaken at exactly the same clumps of cover during the following October; four others were in the same ranges being only 85 to 185 yards from spring trap sites. Six moved 240 to 408 yards and four moved slightly more than 0.25 mile. The average distance for the 20 birds from spring to autumn was 220 yards.

Movement records from spring to autumn, 1943, involved 131 birds. Only 8 were retaken at the same stations, but 26 drifted less than 200 yards, 32 moved up to 0.25 mile, and 51 traveled 0.25 to 0.5 mile. Five were trapped or shot more than a mile from early spring ranges; the longest movement was approximately 7.5 miles. The average movement was 611 yards (0.3 mile).

Two to four members of a late winter covey commonly occupied the same range during two successive winters. In the interval between late winter and autumn, however, most birds scattered and did not return. The distances moved varied greatly between individuals of the same covey and the spread was usually in several directions. Three or more individuals from each of 20 coveys of February 1943 were retaken the following autumn. Circles were drawn on maps with the centers at the late winter banding stations and with perimeters to enclose the spread of all individuals in each of the 20 groups. The radii of these circles averaged 956 (283 to 2,200) yards in length. When members of particular coveys were considered as units, the average spread from February stations was 667 yards. The breeding season dispersal of eight groups (diagrammed on Fig. 1) shows that members of these coveys were well dispersed over most of the 960-acre area in only one breeding season. This spread took place in territory where superior nesting cover was distributed generally, and suggests that dispersal may be appreciable, even in a favorable habitat.

Our nesting studies employed the use of a flushing bar mounted on the front of a pick-up truck (Lehmann and Davis, 1942); this device facilitated the accumulation of reliable data on relative nest density. Initial nesting efforts were usually concentrated on late winter ranges. These concentrations and others later in the season broke up when predation was severe (Lehmann, 1943). Most pairs of quail did not invariably renest after previous nests were destroyed; egg laying was general only after rains. The rainfall in the summers of 1942 and 1943 was staggered, as was the breeding activity. It is believed that the bulk of movement from February to autumn occurred in the intervals of

arrested breeding activity between rains, and that this movement was influenced by predation to an appreciable degree.

Under nearly natural conditions, it appeared that the bulk of mating was among members of a given late winter covey, and that laying began before covey bonds were finally dissolved.

groups might not be better practice than the present general custom in hunting, of passing up small coveys and concentrating shooting pressure on the larger ones.

AUTUMN MOVEMENTS

Attempts were made to trap any particular covey only once during a

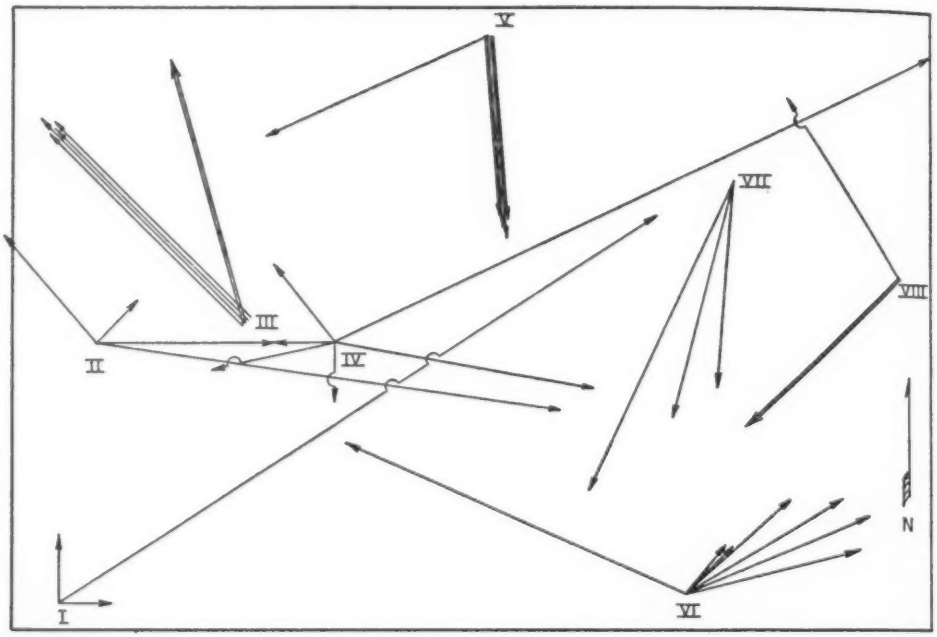

Fig. 1. Breeding season dispersal of eight coveys of bobwhite quail, 1943. W. W. Jones Ranch, Jim Hogg County, Texas. Roman numerals indicate separate coveys and approximate centers of covey ranges in February. Each arrow represents one quail and shows distance and direction of spread from February to autumn. Scale: 1 inch = about 625 feet.

Pairing and breeding seemingly proceeded more rapidly and more orderly in large groups than in those containing 4 or 5 birds. Since the presence of large coveys may facilitate reproduction and since the summer dispersal is appreciable, one is inclined to wonder whether non-disturbance of strategically located large coveys plus a closer kill of small

season in order to keep disturbance at a minimum, but some quail were retaken several times because they joined other coveys; these yielded the following records on short-term movements.

From October 12 to November 21, 1942, one quail was caught twice at the same bush, and 10 others were taken 200 yards or less from original trap

sites. There were 33 retrapped at 200 to 440 yards from previous banding stations; five birds moved more than 0.25 mile. The longest recorded movement of 808 yards, was made by three birds from one covey. The average movement of 49 quail during the autumn of 1942 was 336 yards.

Ninety-seven quail were retrapped from October 9 to November 20, 1943. The average movement was about 396 yards or slightly greater than in 1942. Five were retaken at original trap sites, 35 registered movements of 200 yards or less, 38 traveled from 201 to 440 yards, 10 traveled 440 to 880 yards, and 9 (all from one covey) moved 5,500 to 6,500 yards.

LATE WINTER

In late January and during February, 1943, the average movement of 67 birds was 402 yards. Of these, 17 were retaken at the same stations, 9 moved 200 yards or less, 16 traveled 200 to 440 yards, and 24 (36%, moved 440 to 880 yards. One moved 1.6 miles in a week.

Only 16 quail, too few to provide a good index of movement, were retrapped in late winter 1944; 8 were at original trap sites, 2 less than 200 yards away, 4 traveled 440 yards or less, and 2 moved between 440 to 880 yards. The average movement was 173 yards.

AUTUMN TO LATE WINTER

The 105 birds trapped in the autumn of 1942 and retaken the following January or February were decidedly sedentary, being retrapped within 200 yards or less from the original stations. Forty-eight had traveled 200 to 440 yards, and 25 moved 440 to 880 yards. Two drifted more than a mile and one was killed 6 miles from the study area. Average movement for the group was 324 yards.

Sixty-three quail marked in October and November 1943 were caught in January or February 1944; 14 moved 200 yards or less, 26 moved 201 to 440 yards, and 19 from 441 to 880 yards. Four traveled more than one mile, but remained on or near the study area; average movement of the 63 was 459 yards.

ANNUAL MOVEMENTS

Four birds banded in April 1942 were recaptured 200 yards from the original banding stations approximately one year later. Four others moved less than 440 yards, 2 traveled 440 to 880 yards, one drifted one mile, and 3 moved more than a mile. The average movement was about 850 yards.

In the later winter of 1943–44, there were 22 trapped approximately 200 yards or less from where they were taken the preceding winter; 10 others registered moves of from 201 to 440 yards, 21 moved 440 to 880 yards, and 3 traveled more than one-half mile but less than a mile, and one more than a mile. The average movement of the 57 was 410 yards.

Thirty-one quail caught in the autumn of 1943 were 200 yards or less from where taken the preceding autumn; 33 others were less than 440 yards distant, 16 traveled from 440 to 880 yards, four moved between one-half and one mile, and 5 moved more than 1 mile. The average movement was 473 yards. In 12 months, therefore, the average distance moved by 151 quail was 489 yards, or slightly more than one-fourth mile (Fig. 2).

2-YEAR MOVEMENTS

Four of the birds banded in April 1942 were retaken late in the winter of 1943–44. One was retrapped about 100 yards from the original trapping site; the others were 300, 650, and 2,650 yards, respectively, from their original stations.

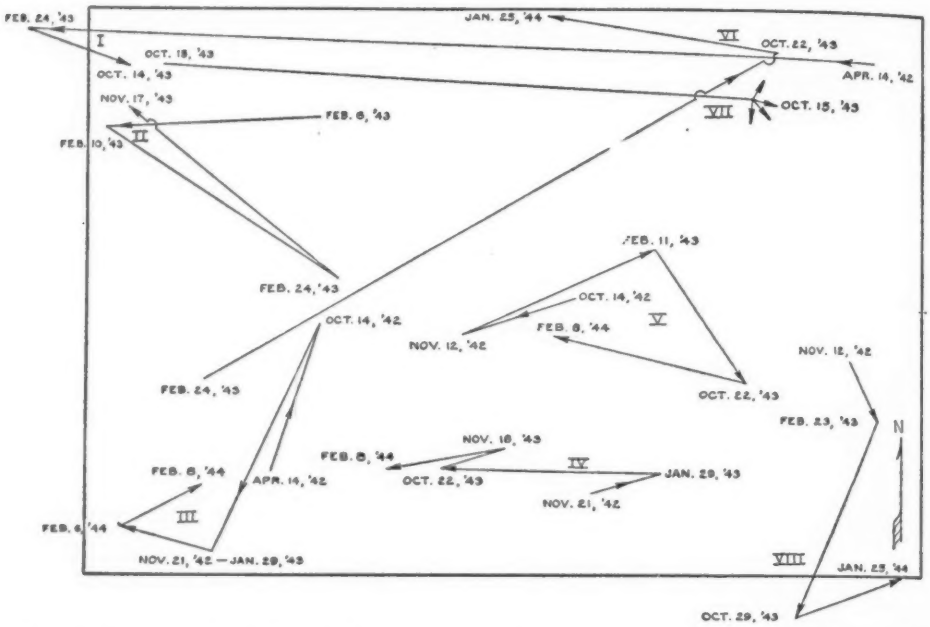

Fig. 2. Movements of individual bobwhites, based on records of banded birds, 1942–44. W. W. Jones Ranch, Jim Hogg County, Texas. Roman numerals designate the birds, and arrows show their movements. Scale: 1 inch = about 625 feet.

MOVEMENTS OF INDIVIDUALS

Definite records of 699 quail showed that some of the birds were sedentary, but that bobwhites are capable of moving relatively long distances in short periods. Of 921 birds banded on the study area from April 1942 through February 1943, 748 (about 81%), were not recovered despite intensive efforts in the autumn of 1943. This suggested that most of them either moved considerable distances from the original banding stations or died. It is thought that most of them moved. Of the 699 individuals that yielded the 787 records of movement, 257 (almost 37%) moved more than one-fourth mile during the short span of our studies. These data make it seem likely that less than half of the quail spend their life span within a quarter mile of their birthplaces.

DIMENSIONS OF HOME RANGE

Some retrap records implied movement almost in a straight line and the dimensions of the home range were not indicated. In other instances the retrapping sites, when projected on maps, made patterns that appeared to be

rough outlines of the home range of the quail. Such patterns should be accepted as more nearly portraying minimum rather than maximum range dimensions because it is improbable that many birds were at the exact outer edges of their territories when they were captured. Furthermore our records outline the ranges of only those birds that were relatively sedentary and remained on or near the 960 acre study area.

From autumn through late winter (4 to 5 months), the home ranges of 20 birds, as portrayed by four or more retrap records, averaged 172 by 532 yards in extent. In approximately 8 months (from late winter to autumn of the following year) there were 14 ranges 640 by 293 yards. The 27 territories outlined for a full year, were 725 by 235 yards; and 20 ranges, in 16 months, averaged 807 by 219 yards. Two birds followed for approximately two years ranged over areas approximately 900 by 400 yards and 200 by 117 yards, respectively (Fig. 2).

Our best data on range and mobility therefore suggest that bobwhite quail, from autumn through late winter, usually have home ranges slightly over one-fourth mile long. With time, the ranges are often extended in length but widened only slightly. Some quail gradually extend their home ranges in a particular direction with time and others change from one area to another. By the end of 16 months, many birds had ranged over strips of territory about one-half mile in length, and most of them may have covered larger areas.

BANDING DATA ON COVEYS

Intensive censuses during the course of banding operations in the autumn of 1942 showed 53 coveys containing approximately 596 quail on the study area; of these, 549 (92%) were trapped and banded. All quail in 43 coveys were caught and only one was missed from each of three other coveys. Two birds escaped from each of three coveys; three birds were not banded in one covey. Misses were not determined with high accuracy in the remaining three coveys; a generous estimate is 35 birds. The total number unbanded was about 47.

Trapping was again thorough in late January and all of February 1943; 540 quail were trapped one or more times each from a population of 619 in 55 coveys. Up to 79 (13%) may have been missed, but probably fewer. Catches were complete in 28 coveys, and only one was missed from each of 11 others. The late winter trapping yielded good checks on 47 of the 55 coveys on the area and fair data for the remainder.

FATE OF AUTUMN COVEYS

Of 166 birds marked during autumn in 18 separate coveys totaling 174 individuals, the late winter trapping captured none. It seemed unlikely that all of them had been killed by predators or died from other causes during the winter, and we concluded that most of them moved from the study area.

Thirteen coveys from which 126 of 138 birds were trapped had dispersed in winter, but remnants of them remained. Four coveys that contained 9, 5, 12, and 18 birds, respectively, in October, were each represented by only one banded bird in February. Two members from another autumn covey of 8 were retaken; each was in a different group. Three of the original 11

members of another covey were still together in late winter; three members of still another of 7 joined a nearby group and then disappeared with it. A fall covey of 21 birds was represented in February by 4 birds as pairs in separate groups. Three of the original 7 members of one covey combined with 2 of the original 5 in another to form a combination which persisted; another October group disintegrated with 2 birds going to one nearby covey, 2 to another, and 9 disappearing. Four birds from each of 2 other coveys aggregating 22 birds in the fall joined with a banded individual from a third covey and an unbanded bird to form one spring group. During winter, therefore, 93 of 126 banded birds in 13 coveys or approximately 74 per cent of the banded quail apparently left the study area or died.

Eighteen coveys trapped in the autumn remained on or near the study area and retained at least half of their original members through the winter; an additional 4 coveys may be so classified if birds missed during spring operations are assumed to have been original covey members. In the fall the 22 coveys contained 284 birds and 257 were banded; in spring they held 251 birds of which 227 were caught. The net decrease during winter, therefore, was 33 birds.

The total membership of 14 of the 22 coveys decreased from 202 to 140 birds. Three were smaller by only one bird; one covey decreased by 2, Three coveys lost 3 birds each, and two coveys each decreased 4. Five birds were lost from two other groups, and the remaining 3 coveys lost 7, 8, and 15 birds, respectively. Loss of original covey members was partially offset by the acquisition of new birds in at least two of the 14 groups.

Two coveys containing 20 birds in the fall also contained 20 individuals in February. One, a group of 9, maintained its original composition, and was the only group among the 55 to do so. The second covey lost 3 birds but acquired 3 others.

Six coveys containing 62 birds in the autumn increased their membership to 91. One covey lost 3 of the original members, but gained 10 unbanded birds. Another lost 4, one of which joined another covey on the project, but gained 8. A third covey lost 2 birds but gained 5 new members for a net gain of 3. Another covey gained 2 new birds, still another lost 3 and gained 14. The sixth covey lost at least 2, but gained at least 4 members.

Membership turnover, even in the most stable groups, therefore, was appreciable. Even if all birds missed in spring operations are assumed to have been banded and original members of the groups from which they were missed, the 22 coveys lost at least 84 of their original 251 birds during the winter. When allowances are made for all of the 47 birds missed in autumn, these 22 coveys gained at least 50 unbanded "new" birds. Turnover in these 22 best groups, therefore, was at least 47 per cent.

Nineteen of the 55 coveys trapped in late winter were "new" coveys in that they contained no banded birds; 9 of the February coveys contained only one or two banded "stragglers." Of the 540 birds caught on the study area in late winter, 277 were unbanded, proving that most of them moved on to the

area after autumn banding was completed. Since only 47 quail were missed in that trapping, ingress during the winter of 1942–43 totalled at least 230 birds.

In late winter 263 banded birds were trapped; no more than 79 birds were missed from the 55 coveys. The total number of original autumn birds present in late winter, therefore, did not exceed 342. A minimum of 254 birds disappeared from the 960-acre area during the winter.

The minimum number of birds moving into the area (230) plus the minimum number lost in winter (254) was 484 quail, or only 112 birds less than the autumn population of 596. The turnover on the study area during the winter of 1942–43 therefore was at least 72 per cent.

Although trapping was thorough in the autumn of 1943, the coverage in spring was incomplete. Only 21 of the 32 coveys present were sampled adequately; 7 of these were "new" groups containing no banded birds. Another covey contained only one banded individual. Eight coveys maintained a semblance of their autumn composition by retaining at least 50 per cent of their members; the 5 others were made up of odds and ends of from 2 to 4 autumn groups. There were 37 birds banded off the study area late in the winter of 1942–43 or in the early autumn of 1943, and retrapped on the study area in January or February 1944; 5 of a covey of 8 banded one-half mile to the west on October 25, 1943, moved in as a group. Banding data for January and February 1944 are incomplete, but indicate covey mixing on a scale comparable to that recorded the previous winter.

COVEY RANGES

It was anticipated that close field reconnaissance, supplemented by banding, would yield excellent data on the ranges of a large number of coveys. Field observation proved to be almost valueless for this purpose, and banding yielded far fewer data than expected; this resulted because many of the groups disintegrated or disappeared while the studies were in progress. Ten coveys were accommodating to the extent that they stayed on the study area from autumn through late winter, remained fairly intact, and were retrapped at least 4 times. As in the case of individual birds, the range boundaries of coveys, as determined by banding, probably were somewhat smaller than those of the actual territories.

For better illustration, actual positions of some ranges were shifted on Fig. 3; sizes, however, were not altered. Ranges "1" to "4" were for the 1942–43 season, and the others for the winter of 1943–44.

Each of the 10 covey ranges was slightly more than one-fourth mile in length and the longest almost one-half mile; the average length was 643 yards. Most ranges were 100 to 200 yards wide, the average width being 178 yards.

Every covey range on the 960-acre area in both 1942–43 and in 1943–44 was overlapped at one time or another by the ranges of one to six other coveys. This led to little if any serious conflict in feeding, roosting, escape, or nesting. When feeding, ordinarily one covey veered its course slightly when another approached; at other times they fed together with only occasional jousts between individuals. In no instances

were fights of a serious nature observed between entire coveys. Five coveys containing more than 70 birds regularly fed together for several weeks during the winter of 1942–43 in an area of less than two acres; 42 birds were once taken together at a single trap. At least parts of two or three coveys could be herded and trapped together during feeding periods in early morning or late afternoon, but during midday rest periods this was almost impossible.

Only in competition for choice midday resting sites did coveys demonstrate any serious intolerance to close association with other groups. Coveys already occupying clumps of "key" loafing cover (Pl. 10, C) usually challenged the approach of others, and trapping efforts that brought two or more groups into the close contact usually resulted in spirited fighting. Different coveys were frequently found loafing in plain sight of each other at opposite ends of mesquite mottes 20 to 30 yards long; again, sometimes 4 or 5 different coveys were observed under small clumps of tasajillo or other choice cover only 10 to 25 yards apart (Pl. 10, D). While such groups almost always defended their identity in midday, they sometimes fed together with little evidence or friction a few hours later. Research in Jim Hogg County therefore emphasized the importance of increasing the headquarters areas for coveys as a method for building up quail populations in otherwise favorable range (Lehmann, 1939).

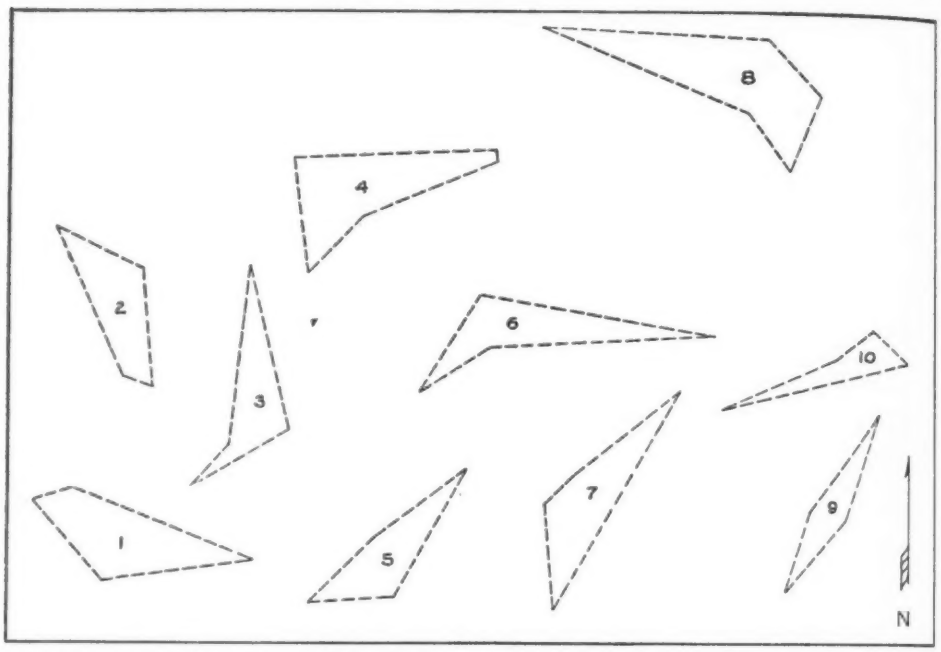

Fig. 3. Approximate boundaries of ranges of 10 bobwhite coveys on study area, W. W. Jones Ranch, Jim Hogg County, Texas. The locations are shifted slightly to facilitate illustration. Scale: 1 inch = about 625 feet.

Errington and Hamerstrom (1936,

p. 313) reported that covey ranges may shrink in size as populations rise, which they interpreted as evidence of intraspecific intolerance. Our studies did not suggest that ranges contract as populations increase; they appeared to remain about the same size or actually expanded.

Some coveys studied during the two successive winters were relatively stable as to both their range and composition, but others were not. Individual quail were not always the units of movement. The turnover in "personnel" was at least 2 coveys at each of 26 of our banding stations in the winter of 1942–43; it was at least 4 coveys at one station, 5 coveys at each of two others, and six coveys at still another. At this last station, 4 distinct coveys, all of about the same size, were trapped between January 11 and February 12, 1943. In contrast to the findings of Errington and Hamerstrom in Iowa (1936, pp. 312–316), there was considerable midwinter shifting of coveys that did not appear to be under stress of starvation or scarcity of cover. Furthermore, the bulk of autumn and winter movements could scarcely be attributed to wandering coveys that had no really suitable place to stay. Mobile birds could hardly have represented, to a material extent, doomed over-populations or those evicted by wholesale destruction of habitat. Indeed, movements during particular periods and fluctuations in densities from one season to another appeared materially independent of habitat conditions. This does not imply that movement and mixing might not have been decidedly greater, if the habitats had changed appreciably. The turnover in quail population was at least 72 per cent on the 960-acre area during the winter of 1942–43. In the absence of banding, there could be no certainty on this point. Bands or other positive markings therefore seem absolutely basic in winter population studies. Bobwhites in many areas may not be as sedentary and as adapted to farm management procedures as has long been supposed.

SUMMARY

The bobwhite quail population of a 960-acre study area in Jim Hogg County, Texas, moved about much more than indicated by published observations of this quail in other regions. Some individuals and coveys were relatively sedentary, but the population as a whole underwent continuous movement.

The banding of 2,509 birds yielded 787 records of movement for 699 birds and proved that some quail moved little for periods as long as two years. On the other hand, it indicated that bobwhites are physically capable of traveling considerable distances, and many of them do so. More than half of the quail evidently moved decidedly more than a quarter mile from their birth places; the bobwhite, as a species, may be decidedly more mobile than previous banding studies suggested. There is also a possibility that the bobwhites of southern Texas are more mobile than the average of the species elsewhere.

Individual birds in winter ranged over strips of territory slightly over one-fourth of a mile long; with time, ranges often extended in length but did not increase greatly in width. Range expansion was sometimes gradual, but certain birds leap-frogged from one territory to another. Most quail, it

appears, are acquainted with territories about one-half mile long by the end of 16 months of life.

Intensive trapping revealed that many coveys disappeared from the study area in winter, and that others disintegrated. Movement during particular periods and fluctuations in quail densities appeared largely independent of habitat conditions. Mixing and shifting in winter could hardly be attributed to doomed over-populations. Only 22 of 55 coveys studied in the winter of 1942–43 both remained on or near the study area and retained 50 per cent of their autumn members. The turnover in these coveys, the most static groups, was at least 47 per cent; it was at least 72 per cent from autumn until late winter, considering the entire autumn population.

Ten winter ranges averaged about 643 yards long by 178 yards wide. All covey ranges over-lapped; intraspecific intolerance to crowding appeared unimportant except in competition for choice resting or "headquarters" cover at midday. Covey ranges did not appear to shrink or expand as populations increased or decreased.

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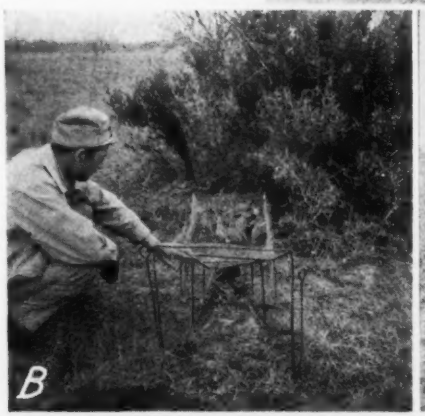
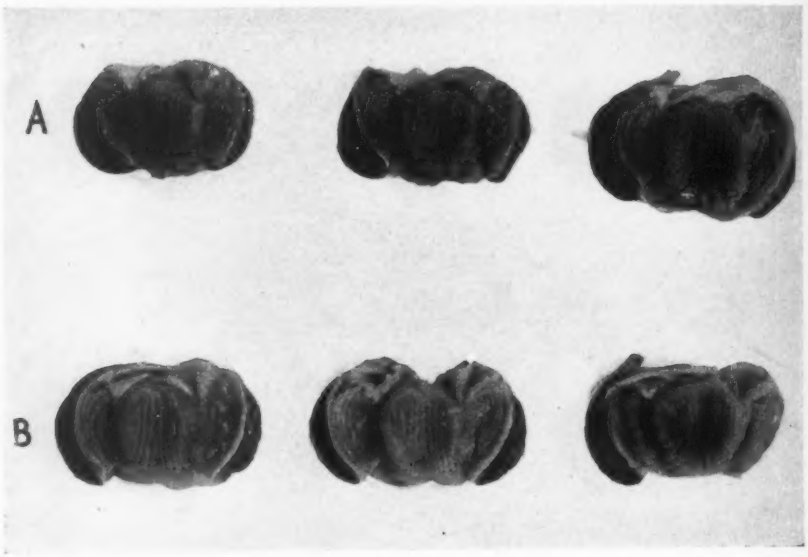


Bobwhite quail. W. W. Jones Ranch, Jim Hogg County, Texas. *A*. Moderately grazed mesquite semi-prairie ranch land of the type on which banding studies were conducted. December 1942. *B*. Covey of bobwhites in the Ward drive-type quail trap. December 1941. *C*. Tasajillo (*Opuntia leptocaulis*), a preferred loafing cover. January 1944. *D*. Several coveys often loafed in plain sight of each other in situations where clumps of choice loafing cover were close together. December 1943.



Gizzards of year-old bobwhite quail. *A*. With access to grit.
B. Deprived of grit during entire lifetime.

MECHANICAL VALUE OF GRIT FOR BOBWHITE QUAIL

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The question of the value and function of grit in the digestive processes of gallinaceous birds has been debated ever since the latter part of the eighteenth century when Spallanzi (1784) remarked: "We may reasonably conclude that the collecting of pebbles by chickens is less the effect of choice than stupidity." Generally grit is considered to have two functions in avian nutrition, namely (1) assisting the gizzard in the grinding of food, and (2) furnishing necessary minerals for metabolism and reproduction. For grinding, hard non-friable insoluble particles, such as quartz and flint, are the more desirable; whereas for the purpose of supplying nutrients, a soft easily-crumbled material, such as limestone and oyster shell, is required. This paper deals with grit solely as a grinding agent.

Strong convictions on the abrasive value of grit have been succinctly expressed by a number of writers on gamebird propagation. Carnegie (1906) emphasized his belief in the need of grit for pheasants and partridges by the pithy statement: "It is of little use feeding them properly if the means for masticating the food be not provided"; and Tegetmeier (1913) admonished propagators that "one of the essentials to health in pheasants is an adequate supplement of suitable grit, and it should be remembered that this is necessary at the earliest stages of their existence. If deprived of this a bird will soon deteriorate in condition owing to the gizzard being unable to perform its function." Although Leopold (1936) presented data to prove that gamebirds consume an appreciable quantity of grit, he seemingly was not completely convinced that grit is essential. Regarding quail, for example, Leopold wrote: "Quail are commonly believed to require grit. *If they do* [Italics ours] then ledges of rock or gravel, or windfalls bearing gravelly soil, are necessary during snows."

Considerable doubt, however, has been cast on the mechanical value of grit for gallinaceous birds through carefully controlled studies on poultry by Buckner and Martin (1922), Kaupp and Ivey (1923), and Buckner, Martin and Peter (1926). Grit was found to be non-essential to the growth and reproduction of chickens. In fact, birds which did not receive grit appeared to utilize coarse ground feeds and whole corn and wheat as effectively as those that had access to grit.

Of even greater interest is the astounding evidence by Burrows (1936) and Fritz, Burrows and Titus (1936) that even the gizzard itself is not essential to life. As might be expected gizzardectomized birds digested coarse feeds much less efficiently than did normal fowl, but on finely ground mashes they showed little difference in the efficiency of feed utilization.

As to the retention or grit in the digestive tract, Handley (1931) pointed out that when grit can be easily obtained a portion of the grit in the gizzard is passed on daily, whereas if the

supply is cut off the particles in the gizzard may be conserved. Experimental evidence by Errington (1931) and Gerstell (1942) seems to prove conclusively that gamebirds are able to retain previously ingested grit for six weeks or longer after being deprived of a further supply. Gerstell also found that enforced abstinence by both pheasants and bobwhites, for two and a half months of winter weather, can be endured without serious ill effects.

There are times when hard seeds are utilized in the same manner as grit by such wild birds. The factors influencing such substitution, according to Beer and Tidyman (1942), are the shape, hardness, and availability of seeds, and the food preferences of the birds. Handley (1931) asserted that bobwhite quail consume little grit when hard seeds, such as those of loblolly pine or wild cherry, form a main item of the diet.

Most of the evidence presented above strongly indicates there is little need of fear that gallinaceous birds in the wild may suffer from a grit deficiency, despite qualms of some game conservationists to the contrary. Practically all earlier controlled studies on the essentiality of grit have been conducted with domestic birds. Those here reported on bobwhite quail (*Colinus virginianus*) were made to determine whether this related wild species can retain grit during weeks of deprivation and substitute hard seeds for grit, and whether it can survive, grow and reproduce on a *total* lack of grit.

GRIT DURING GROWTH

Results from two groups of experiments are presented. In both, the ration was a well-balanced chick diet containing 28 per cent crude protein, 1.1–1.2 per cent calcium, 0.7 per cent phosphorus, enough additional manganese to furnish 100 p.p.m. of the diet, and sufficient quantities of the vitamins to satisfy the known or assumed requirements of the birds. The cereal in the diet was granular as obtained from a hammer mill with a 3/32 inch-mesh screen. This ration was fed ad libitum. Half of the quail in each group was given hard non-friable coarse sand in special feeders from the time they were placed in the brooders, simultaneously with the supplying of the ration. Grit of larger particles was fed as the birds grew older. The other half of the quail, similar to the first in age and pedigree, were fed no grit during the growing period. The birds were kept on wire floors at all times.

Group A, of 268 bobwhites, was carried on experiment for 8 weeks; at the end of that period the results were as follows:

	Grit	*No grit*
Survival:		
Numbers	84	91
Percentage	*63*	*68*
Victims of picking:		
Number	28	8
Percentage	*21*	*6*
Average bird-weight (grams)	111	113
Feed consumed per bird per day (grams)	7.0	6.5
Feed per gram gain in body weight (grams)	3.7	3.4

The chicks that received no grit equalled or surpassed those on grit as to survival, vice prevention, rate of growth, and efficiency of feed utilization.

Group B, of 1104 quail, was carried for 10 weeks. Unfortunately the feed records were not kept separately for

the two lots, so that differences in feed consumption and efficiency of feed utilization are not apparent. Of the birds on grit 58 per cent survived and averaged 144.6 grams in weight, whereas 62 per cent of those without grit survived and averaged 144.4 grams in weight. Eight (1½%) of the former were victims of picking and 22 (4%) of the latter. Again, birds without grit were maintained in as good condition as those receiving pebbles.

GRIT DURING WINTER

Winter, especially in the range of the northern bobwhite, where snow and ice may blanket the ground for weeks at a time, is the season when gamebirds are supposed by many to suffer from grit defficiency.

During November 1943, 60 quail raised without grit and 120 quail with grit, from Groups A and B, were distributed in nine wire-floored maintenance pens, 20 birds per pen. Those without grit were kept separate from the others and continued on a gritless regimen. Of the 120 raised with grit, those in three pens were supplied with grit, and in the other three were deprived of grit for the 20 weeks of the experiment.

All nine pens received the following feed mixture ad libitum (parts by weight):

Wheat, whole	90.9
Millet, whole	45.4
Milo, whole	45.4
Soybeans, whole, Wilson black	45.4
Field peas, whole, Canada	22.7
Vetch, whole	22.7
Alfalfa leaf meal	13.6
Bonemeal, finely ground	4.5

The alfalfa leaf meal was incorporated to supply pro-vitamin A to the birds. Yellow corn ordinarily would be a more desirable source of carotene in such a mixture of whole seeds, but could not be used for three reasons: (1) regular sized kernels are too large to be used by quail in confinement on wire floors, (2) regular sized kernels when cracked are too easily macerated and digested, and (3) popcorn kernels, which are right for size, then were unobtainable.

During the third week, heavy mortality suddenly developed. Post mortem revealed symptoms of vitamin A deficiency. Analysis of the crop contents of dead birds disclosed practically no alfalfa leaf meal. The quail apparently were avoiding their only source of pro-vitamin A. Mortality was checked almost instantaneously by the addition to the diet of 1 per cent of fortified vitamin A and D feeding oil which had an adhesive effect in binding the alfalfa leaf meal to the seeds, and including chopped cabbage and kale in the ration. The fresh greens were discontinued after one week, but the oil was fed throughout the remainder of the study.

A remarkable feature of this mortality from A-avitaminosis was that the highest death rate occurred, by a significant differential, among the birds receiving grit. The results, as to percentage mortality, were as follows:

	Grit regimen		
	None since hatching	*Withdrawn*	*Fed*
Pen 1	0	25	45
Pen 2	6	0	100
Pen 3	26	35	70
Combined pens	11	22	72

It seems highly improbable that the grit was directly responsible for the higher mortality. In fact, some grit

from the same lot was used in other experiments before and after the one herein reported, without producing deleterious effects. In any event, it is safe to conclude that birds without grit since hatching survive as well as those having access to gravel.

A majority of the birds gained in weight during the first 12 weeks of the experiment (Nov. 18 to Feb. 12) and lost weight during the last eight weeks as they approached the breeding season:

	Grit regimen		
	None since hatching	*Withdrawn*	*Fed*
Final weight, grams	186	183	182
Gain over initial weight, grams	15	21	23
Percentage	*9*	*13*	*15*

The birds without grit since hatching showed greater gains through the eighth week than those from which grit was withdrawn at the start of the experiment, but not as great as those on grit. The loss in weight of the first mentioned stock was slightly more accelerated during the last two months than that of the other groups. Nevertheless, the final weights of the gritless birds are the highest of the experiment. Considering the heavy mortality that existed, however, these differences cannot be considered significant.

The feed consumption per bird per day for the duration of the study was exactly the same for all three groups, 16.6 grams. This figure includes 0.8 gram of grit taken by the birds receiving grit. The consumption of grit was higher during the first part of the experiment than at the close: 1.5 grams per bird per day, or 1 part of grit to 12 parts of seed mixture, as compared with 0.5 gram per bird per day, or 1 part of grit to 30 parts of seed mixture.

Post mortem examination of birds raised without grit showed complete digestion of the whole seeds and no lesions in the gizzards. The gizzards of the birds deprived of grit at the start of the winter experiment still retained large quantities of grit after five months.

GRIT DURING BREEDING SEASON

Pairs of birds from each of the three groups compared during the winter (without grit since hatching; without grit during winter; and continued on grit) were distributed at random in the breeding pens during the following May. All then received grit and a good breeding mash.

The mortality during the breeding season was 15, 14 and 40 per cent respectively; and egg production per bird was 58, 67 and 51. Thus the absence of grit during the winter months, or since hatching time, had no adverse effect on the subsequent health or reproductive activity.

At the time of the regular breeding work, 12 pairs of bobwhites that had received no grit during their lifetime were continued on the whole seed diet used in the maintenance experiment. They received a finely ground mineral mixture of limestone, bonemeal, and salt, but no grit. Two females died during the season, one pair resorted to self-picking, and one pair developed the vice of egg-eating. A majority of the birds, however, apparently lived normal healthy lives and produced an average of 37 eggs per hen, although the diet was lacking entirely in animal protein. Fertility of the eggs was high,

93 per cent of all eggs set, but the hatchability of the fertile eggs was low, only 26 per cent. This low hatch was undoubtedly due to an inadequate intake of Vitamin A or its precursor, carotene, despite the presence of vitamin A and D feeding oil fortified or alfalfa leaf meal in the diet. Assay of the livers of the breeders at the close of the experiment revealed poor storage of this important dietary factor. The oil on the surface of the whole seed probably oxidized very rapidly and lost much of its potency. The gizzards of the quail that had lived for over a year without grit showed no lesions, but had thicker, smoother linings than those from bobwhites with access to grit (Pl. 11). The feed consumption per bird per day was 16 grams, the same as that of birds on a mash with grit.

CONCLUSIONS

Grit as a grinding agent in the gizzards of bobwhite quail is not essential for the growth, welfare, or reproduction. Seeds such as wheat, millet, milo, soybeans, field peas, and vetch can be successfully macerated and digested without the aid of grit. When very hard seeds are ingested in the wild, apparently the seeds themselves serve in the capacity of grinding agents.

SUMMARY

An investigation on the need of grit as a grinding agent in the digestive processes of bobwhite quail was conducted with 1,372 pen-raised birds at the Patuxent Research Refuge, Bowie, Maryland. Some of the stock was reared, maintained through winter, and bred without access to any grit, although the diet after the tenth week consisted of whole seeds.

As to survival, weight, and efficiency of feed consumption, the birds without grit during their period of growth equalled those with access to grit. Such birds, when continued on a gritless regimen during the winter, survived and maintained their weight as successfully as birds on grit. There were no gizzard lesions, and the digestion of whole seeds was satisfactory. Subsequent health and reproduction were unaffected by the absence of grit.

The quail reared with access to grit retained an appreciable supply of grit in their gizzards for five months after being deprived of it.

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WINTER FOOD OF BOBWHITE QUAIL IN VIRGINIA[1]

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During the winters of 1929 to 1931 over 500 crops of the bobwhite quail (*Colinus virginianus*) were collected by Handley throughout Virginia; the contents of these were examined in 1938 by Baldwin. Although the resulting data apply to conditions about 15 years ago, the information secured is of value, if only for comparison with present and future studies to show the changing trends in food conditions.

The food of the bobwhite quail has been widely investigated throughout the bird's range, but this is the first extensive account of Virginia conditions. Previously data for Virginia were presented by Judd (1905), who examined some crops, but grouped the findings with those of quail collected in eight other states.

MATERIALS

The contents of 548 crops, collected during the hunting season, November 15 to January 31, were examined. These were secured from sportsmen and game wardens, chiefly during 1929 to 1931, although a few were collected in later years. The method of laboratory examination was that described by Handley in Stoddard (1931), and was done in the Food Habits Laboratory of the U. S. Fish and Wildlife Service. Of the crops examined, 53 were discarded because the contents lacked sufficient volume. The resulting compilations are based on 495 as to monthly records and 490 by regions (5 lacked locality records).

The results are assembled to show monthly differences in quail food habits and also to indicate sectional differences. The boundaries of these geographic sections are indicated on Figure 1. For convenience, the division lines are plotted along county boundaries. It

[1] Virginia Cooperative Wildlife Research Unit: Virginia Commission of Game and Inland Fisheries, Virginia Polytechnic Institute, American Wildlife Institute, and U. S. Fish and Wildlife Service, cooperating. Assistance with identification of food items was given by Clarence Cottam, Alec C. Martin, Lawrence W. Saylor, and Misses Phoebe Knappen and Alma Swords; A. B. Massey gave advice on plant distribution in Virginia.

is customary to consider the "fall line" in eastern Virginia as the boundary between the Coastal Plain and Piedmont, but a more arbitrary division based on a compromise between general forest type and general soil type was selected. The Piedmont-Mountain division line follows, for the most part, the first 2500-foot contour line east of the mountains; it is the natural division between the central hardwoods and the northern hardwoods forest types, as set forth by Mattoon (1936).

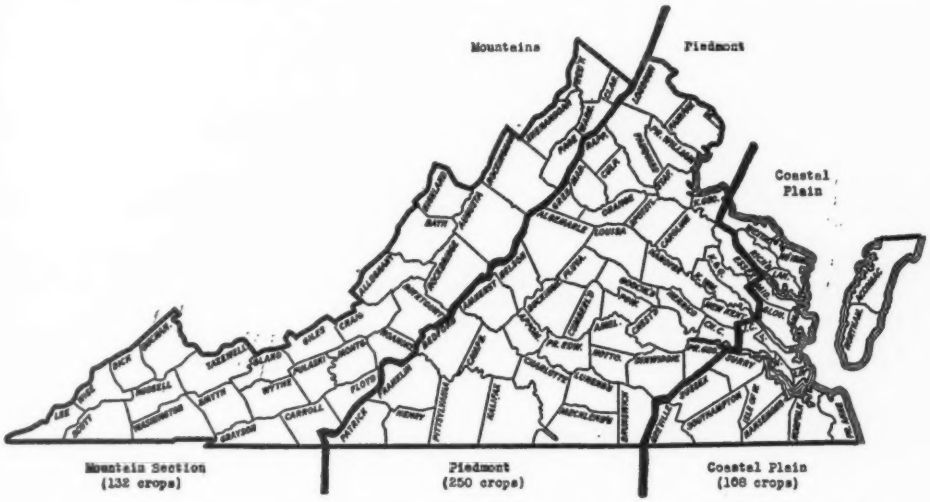

Fig. 1. Map of Virginia showing county divisions and arbitrary delineation of the three natural regions.

The Coastal Plain section shown on the map is largely devoted to growing peanuts, cotton and truck crops; the Piedmont is used for dairying, general farming, tobacco, fruit, and livestock; and the Mountain section, including the Great Valley, is used for livestock and general farming.

RESULTS

A detailed record of the contents of each quail crop was made, counting the items and measuring the volume of each food item. Volumetric percentages for each food then were calculated. In the 495 crops, 253 plant and 198 animal species or groups were identified, indicating the varied feeding habits of the quail even under winter conditions. A detailed report of these is included in the senior author's thesis deposited in the library of Virginia Polytechnic Institute.

When the volumetric percentages of the monthly distributions are compared with those of the sectional distributions (Tables 1–3) there is seemingly a discrepancy between the "average" percentages of each. This results from the fact that the volumetric percentages for the monthly occurrences are figured on the basis of 495 crops, whereas those for the sectional occurrences are figured on a 490 crop basis. The chief differences between

comparable "average" columns, however, are due to the method of calculation. These particular averages were obtained by simply adding up the three monthly or sectional percentages and dividing the totals by three. This followed. Food items are tabulated by common names and their equivalent scientific names are presented in the discussion.

No detailed attempt will be made to discuss the varying importance of each

TABLE 1.—FOODS UTILIZED BY BOBWHITE QUAIL IN VIRGINIA DURING WINTER SEASON. (all figures are percentages by volume)

Months and Sections	Nov.	Dec.	Jan.	Ave.	Coastal area	Piedmont	Mountain	Ave.
Number of crops	115	267	113	495	108	250	132	490
Native and naturalized legumes	9.7	29.1	48.8	29.2	24.8	36.9	17.9	26.5
Ragweed	31.5	22.1	10.3	21.3	15.0	20.6	27.5	21.1
Cultivated legumes	12.7	12.2	15.5	13.5	31.4	10.2	3.4	15.0
Cultivated grains	16.6	10.3	7.4	11.4	9.7	5.7	24.9	13.4
Mast	12.4	10.4	6.1	9.6	6.9	9.4	12.9	9.7
Miscellaneous seeds	6.4	8.0	5.1	6.5	4.7	6.9	8.4	6.7
Fruits	4.8	5.1	2.9	4.3	3.6	6.2	2.2	4.0
Forage	.5	1.1	3.0	1.5	1.3	1.5	1.1	1.3
Grasses	.6	.8	.6	.7	1.2	.8	.2	.7
Total vegetable food	95.2	99.1	99.7	98.0	98.6	98.2	98.5	98.4
Orthoptera	3.4	.5	trace	1.3	.6	1.4	.6	.9
Misc. animal matter	1.4	.4	.3	.7	.8	.4	.9	.7
Total animal food	4.8	.9	.3	2.0	1.4	1.8	1.5	1.6

resulted in averages differing slightly for the same foods in the various tables, a less accurate result than would be secured by recalculating averages from total State-wide food volumes in relation to total number of crops. Of greatest interest are the trends of food consumption in the monthly and sectional distributions, and the "averages" of these trends are presented for their more general value.

DISCUSSION

The nomenclature of the plants, except for the grasses, follows Gray's *New Manual of Botany* (1908); for the grasses Hitchcock's *Manual of the Grasses of the United States* (1935) was

of the food items listed (Tables 2 and 3), as the changing conditions from month to month, and section to section, are obvious. Thus, the small pods and seeds of Japan clover (*Lespedeza striata*) were only one per cent of the total November food, but increased to eight per cent in the December food and 20 per cent of the January total. The data for the same species in Table 3 show that it was most important in the Piedmont section. The groups presented in Table 1 will be discussed briefly.

NATIVE AND NATURALIZED LEGUMES

Under this heading were included 25 species or groups of the Leguminosae

TABLE 2.—THE MOST IMPORTANT WINTER FOODS OF BOBWHITE QUAIL IN VIRGINIA, BY MONTHS.[a]
(all figures are percentages by volume)

Species	Three-month average		November		December		January	
	Rating	Percentage	Rating	Percentage	Rating	Percentage	Rating	Percentage
Ragweed	1	*21.3*	1	*31.5*	1	*22.1*	4	*10.3*
Japan clover	2	*9.7*	16	*1.2*	2	*8.3*	1	*19.7*
Soybeans	3	*7.6*	5	*5.3*	5	*5.4*	3	*12.0*
Partridge peas	4	*6.2*	13	*1.5*	12	*2.2*	2	*14.9*
Cowpeas	5	*5.1*	4	*6.1*	4	*5.8*	6	*3.5*
Wheat	6	*4.0*	2	*7.8*	7	*4.3*	—	—
Oaks	7	*3.7*	7	*4.8*	8	*3.5*	9	*2.7*
Beggarweeds	8	*3.6*	14	*1.4*	6	*5.3*	5	*4.2*
Ash	9	*3.6*	3	*6.3*	15	*1.8*	8	*2.7*
Corn	10	*3.4*	6	*5.0*	13	*2.1*	7	*3.1*
Rye	11	*2.4*	8	*3.2*	11	*2.3*	14	*1.7*
Black locust	12	*2.3*	18	*1.0*	3	*6.0*	—	—
Jewelweed	13	*1.8*	10	*2.8*	18	*1.6*	19	*1.2*
Vetch	14	*1.3*	—	—	19	*1.3*	10	*2.6*
Hog peanut	15	*1.3*	—	—	16	*1.8*	11	*2.2*
Pines	16	*1.1*	15	*1.2*	14	*2.0*	—	—
Grasshoppers	17	*1.0*	9	*2.9*	—	—	—	—
Sweet gum	18	*1.0*	—	—	9	*2.9*	—	—
Smartweeds	—	—	11	*1.9*	—	—	—	—
Persimmon	—	—	12	*1.8*	—	—	—	—
Peanuts	—	—	17	*1.1*	—	—	—	—
Spanish needles	—	—	—	—	10	*2.8*	—	—
Honeysuckle	—	—	—	—	17	*1.5*	20	*1.2*
Day-flower	—	—	—	—	20	*1.1*	—	—
Bush clovers	—	—	—	—	—	—	12	*2.0*
Skunk cabbage	—	—	—	—	—	—	13	*1.7*
Sorghum	—	—	—	—	—	—	15	*1.6*
Blue curls	—	—	—	—	—	—	16	*1.6*
Milk peas	—	—	—	—	—	—	17	*1.4*
Clover leaves	—	—	—	—	—	—	18	*1.2*
Unident. leaves	—	—	—	—	—	—	21	*1.0*
Number of crops examined	495		115		267		113	

[a] Figures below 1.0 per cent omitted.

that provided seeds in the quail's diet. Chief among these were the hog peanut (*Amphicarpa monoica*), ground nut (*Apios tuberosa*), partridge peas (*Cassia chamaecrista* and *C. nictitans*), beggarweeds (*Desmodium*), milk peas (*Galactia*), native bush clovers (*Lespedeza*), Korean lespedeza (*L. stipulacea*), Japan clover or common lespedeza (*L. striata*), black locust (*Robinia pseudoacacia*), wild trailing beans (*Strophostyles helvola* and *S. umbellata*), and vetch (*Vicia*).

The introduced lespedezas (*L. stipulacea* and *L. striata*) were grouped with the native legumes because they have become naturalized in large areas of Virginia. Vetch was here considered to represent the native species although cultivated vetches may have occurred in some of the stomachs. Clovers (*Trifolium*) were excluded from this

group and listed under green "forage" while the cultivated legumes were considered separately.

Together, the native and naturalized legumes were the most important source of winter food for the bobwhite. The seeds of this group increased from 10 per cent of the total November food to 29 per cent in December and to 49 per cent in January. Sectionally, the Piedmont was the best source of these materials.

Japan clover, also known as common lespedeza, was the most important legume in this group. It has become widely distributed as a result of original introduction for hay and grazing. Most of the quail crops were collected in 1929–31, but a small series taken in 1937–38 showed Korean lespedeza to be of great importance. This plant, as it becomes established even more abundantly throughout Virginia, may surpass Japan clover in importance as a

TABLE 3.—THE MOST IMPORTANT WINTER FOODS OF BOBWHITE QUAIL BY GEOGRAPHIC AREAS IN VIRGINIA.[a]
(all figures are percentages by volume)

Species	Statewide average		Coastal Plain		Piedmont		Mountain Section	
	Rating	Percentage	Rating	Percentage	Rating	Percentage	Rating	Percentage
Ragweed	1	*21.0*	2	*15.0*	1	*20.6*	1	*37.5*
Soybeans	2	*8.7*	1	*20.1*	7	*3.2*	10	*2.9*
Japan clover	3	*6.8*	18	*1.1*	2	*16.2*	9	*3.0*
Partridge peas	4	*5.2*	3	*11.3*	5	*4.2*	—	—
Cowpeas	5	*5.1*	4	*8.4*	3	*6.9*	—	—
Wheat	6	*5.0*	11	*1.9*	11	*2.1*	2	*11.0*
Black locust	7	*4.3*	6	*4.8*	—	—	4	*8.1*
Corn	8	*3.9*	5	*6.2*	—	—	6	*5.5*
Beggarweeds	9	*3.9*	9	*2.4*	4	*5.0*	7	*4.2*
Oaks	10	*3.5*	7	*3.2*	6	*3.5*	8	*3.7*
Ash	11	*3.5*	—	—	17	*1.6*	3	*8.8*
Spanish needles	12	*1.9*	—	—	—	—	5	*5.6*
Jewelweed	13	*1.8*	15	*1.5*	13	*1.9*	12	*1.9*
Rye	14	*1.7*	—	—	8	*2.5*	11	*2.7*
Sweet gum	15	*1.4*	10	*2.0*	9	*2.3*	—	—
Pines	17	*1.2*	12	*1.8*	14	*1.8*	—	—
Hog peanut	18	*1.1*	—	—	15	*1.7*	14	*1.6*
Vetch	16	*1.3*	13	*1.7*	10	*2.2*	—	—
Peanuts	19	*1.0*	8	*2.9*	—	—	—	—
Honeysuckle	—	—	14	*1.5*	—	—	—	—
Buckwheat	—	—	16	*1.2*	—	—	—	—
Ground nut	—	—	17	*1.1*	—	—	—	—
Bush clovers	—	—	—	—	12	*1.9*	—	—
Milk peas	—	—	—	—	16	*1.6*	—	—
Dogwood	—	—	—	—	18	*1.5*	—	—
Korean lespedeza	—	—	—	—	19	*1.4*	—	—
Grasshoppers	—	—	—	—	20	*1.3*	—	—
Wild Trailing beans	—	—	—	—	21	*1.2*	—	—
Blue curls	—	—	—	—	22	*1.2*	—	—
Persimmon	—	—	—	—	23	*1.1*	—	—
Foxtail millet	—	—	—	—	—	—	13	*1.8*
Oats	—	—	—	—	—	—	15	*1.2*
Number of crops examined	490		108		250		132	

[a] Figures below 1.0 per cent omitted.

quail food-plant. Likewise, food habits investigations several decades from now may find these species partially replaced in importance by such relatively "newcomers" as *Lespedeza bicolor* and *L. cyrtobotrya*.

RAGWEED

Seeds of the common ragweed (*Ambrosia artemisiifolia*) occurred in 315 crops, and in such a volume that this species was easily the most important winter food-plant in Virginia. It declined in importance through the three winter months, and from the mountainous area throughout the State to the coast. The sectional differences reflect the great abundance of this plant in the western part of the State as a result of grain production, ragweed being an abundant volunteer in fields after the summer grain harvest.

Throughout Virginia the growing season of 1930 was exceptionally hot and rainless (38% normal rainfall in July and 35% in August: Evans, 1930). Even during the growing season of 1929, the north-central counties experienced drought conditions until October, and the yield of farm crops in that area was seriously reduced (Evans, 1929). Since ragweed will make seed under drought conditions when other plants are unable to do so, it is highly probable that the dry 1929–30 growing seasons resulted in the production of less cultivated crops, legumes, and miscellaneous seeds, and the consumption of more ragweed seeds by quail than would normally occur.

The comparatively large woody seeds of the giant ragweed (*A. trifida*) occurred only once in all of the crops, and this was only one seed. Although this plant is common, its large and sharply-pointed achenes must be a recognized menace to the quail.

CULTIVATED LEGUMES

This group includes the peanut (*Arachis hypogea*), kidney bean (*Phaseolus vulgaris*), soy bean (*Soja max*), and cowpea (*Vigna sinensis*). The kidney bean was of little importance. As a group, the cultivated legumes were consistently important throughout the winter months. The sectional differences are interesting: 31 per cent of the total Coastal Plain food, 10 per cent of the Piedmont total, but only three per cent in the Mountain section. As with ragweed and the grains, this is a good illustration of the relation of quail food habits to sectional agricultural practises, for these crops are most commonly planted in the eastern part of the State. Soybeans and cowpeas each occurred in 44 of the 495 quail crops.

When the average volumetric percentages of the cultivated and native legumes are added, legumes make slightly more than 40 per cent of the total volume of food taken by quail in these winter months.

CULTIVATED GRAINS

Seeds of all cultivated grasses that occurred are included in this group; in order of importance, these were wheat (*Triticum aestivum*), corn (*Zea mays*), rye (*Secale cereale*), oats (*Avena sativa*), foxtail millet (*Setaria italica*), sorghum (*Sorghum vulgare*), and barley (*Hordeum vulgare*). The amount of grain eaten decreased during the winter, just as with ragweed; this is most likely a result of decreasing availability rather than selective feeding. As a group, these cultivated crops were most important in the mountain counties, the region of greatest grain production.

MAST

Under this heading are grouped the seeds of the pines (*Pinus*), alder (*Alnus*), birch (*Betula*), American hornbeam (*Carpinus caroliniana*), beech (*Fagus grandifolia*), oaks (*Quercus*), witch hazel (*Hamamelis virginiana*), sweet gum (*Liquidambar styraciflua*), maples (*Acer*), and ash (*Fraxinus*). The tables show which of those occurring were most important. Oaks were the best statewide source of mast. The amount taken decreased from month to month, and its importance also decreased from the mountainous section to the coast.

MISCELLANEOUS SEEDS

A large number of plant species in this group contributed seeds to the winter diet of the quail. Ragweed being of such importance, was not included here. Many species of the Cyperaceae, Caryophyllaceae, Cruciferae, Euphorbiaceae, Umbelliferae, Labiatae, and Compositae were represented, chiefly in minor amounts.

Species contributing over one per cent (volumetrically) of the total food for any month or region were skunk cabbage (*Symplocarpus foetidus*), day flower (*Commelina*), knotweeds and smartweeds (*Polygonum*), jewelweeds (*Impatiens*), blue-curls (*Trichostema dichotomum*), and Spanish needles (*Bidens*). Approximately 0.1 per cent of the total food under this heading was unidentified vegetable matter. The importance of these seeds, as a group, was consistent throughout the three months, but it increased sectionally from the coast to the mountains.

FRUITS

Here are grouped both the hard and fleshy fruits of the red cedar (*Juniperus virginiana*), wax myrtle and bayberry (*Myrica*), sassafras (*Sassafras varifolium*), apple (*Pyrus malus*), rose (*Rosa*), sumac and poison ivy (*Rhus*), Virginia creeper (*Psedera quinquefolia*), grape (*Vitis*), dogwood (*Cornus florida*), black gum (*Nyssa sylvatica*), persimmon (*Diospyros virginiana*), and honeysuckle (*Lonicera japonica*). This group was taken chiefly in December and in the Piedmont section. The fruits of honeysuckle, dogwood, and persimmon were taken in the greatest amounts.

FORAGE

Thirty-five species and groups of plants provided green vegetation in the winter diet. As the season advanced, the take of green forage increased, but the percentage was about the same for all three sections. The principal forage species were sorrel (*Rumex*) and clovers (*Trifolium*), the former occurring in 85 and the latter in 149 of the 495 crops.

GRASSES

Included here are both native and naturalized grasses, exclusive of cultivated forms. Thirty-six species and groups were identified, and of these only certain species of *Digitaria*, *Panicum*, and *Paspalum* were of importance. As a group, the spikelets and seeds of grasses contributed only a small volume to the diet during the three months, but their occurrence was consistent. They were most important in the Coastal Plain and least used in the Mountain section.

TOTAL VEGETABLE FOOD

The total vegetable food increased from 95.2 per cent in November to 99.1 per cent in December and to 99.7

per cent in January. There was about the same percentage throughout the three regions.

TOTAL ANIMAL FOOD

Animal matter made 4.8 per cent of the November food, decreasing to 0.9 per cent in December, and to 0.3 per cent in January. Under Virginia conditions it is to be expected that insects and related groups would be less available in January than in November.

The Orthoptera provided about two-thirds of the animal food, being chiefly of short-horned grasshoppers (*Melanoplus*). Crickets (Gryllidae) were found principally in quail crops from the Coastal Plain and grasshoppers (Acrididae and Tettigoniidae) chiefly in those of Piedmont and Mountain birds.

True bugs (Heteroptera), leafhoppers and their kin (Homoptera), and beetles (Coleoptera) were represented by many species, of which only a few comprised more than a trace of the total food volume. Of the Hymenoptera, the ants (Formicidae) were represented by many species but provided no bulk to the diet. They included representatives of *Aphaenogaster* in 34 crops, *Prenolepis* in 54, and *Lasius* in 56 crops.

Spiders (Araneida) were taken chiefly in the Mountain area and least in the Coastal Plain. Both centipedes (Chilopoda) and the millipedes (Diplopoda) were eaten in small amounts consistently throughout the three months and the three regions. Other groups of invertebrates were represented, but of little importance.

SUMMARY

The contents of 495 crops of the bobwhite quail (*Colinus virginianus*) collected throughout Virginia between November 15 and January 31 were examined.

The total food comprised 98 per cent vegetable matter and two per cent animal matter.

Marked variations occurred in the volume consumed from month to month and section to section for certain species and groups of food items.

The native legumes were the most important source of food followed, in order of importance, by common ragweed, cultivated legumes, cultivated grains, mast, miscellaneous seeds, fruits, animal matter, forage, and native grasses.

Native and cultivated legumes together made over 40 per cent of the total winter food.

More than 25 per cent of the diet was drawn from cultivated crops of all kinds, and a large additional percentage resulted from agricultural practices that encouraged the growth of ragweed and Japan clover (common lespedeza) throughout the Virginia countryside.

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EXPERIMENTAL ANALYSIS OF METHODS FOR MEASURING SMALL MAMMAL POPULATIONS[1]

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Two different procedures for censusing small mammals are in current use, the live-trapping and snap-trapping methods. The results obtained by these two are of such widely divergent magnitudes as to cast doubt on the value of either, and the tests described here were designed to make a direct comparison of them.

The experiment was conducted on the Patuxent Research Refuge of the U. S. Fish and Wildlife Service in Prince George's County, Maryland, during September 1945. The woodland deer mouse (*Peromyscus leucopus*) was chosen as the experimental animal because of its rather large numbers, its readiness to enter traps, and its adaptability to marking.

A circular 17-acre area (488-foot radius) was laid off in a typical section of bottomland forest. The experimental area extends to within 50 feet of the Patuxent River on the north and nearly to the river bluff on the south, but to the east and west is continuous with habitat of a similar type for several miles.

Live Trapping

In the live-trapping method as now generally used a quadrat of several acres is trapped and the animals marked and released until all or nearly all individuals taken are ones that have been caught before. Population estimates are calculated from these data (see especially Dice, 1941; Burt, 1940; and Blair 1940). Within the 17-acre experimental area, 293 Sherman metal box traps were placed at about 50-foot intervals. Care was taken to have them in favorable sites, near trees, brush, logs, etc. They were baited with rolled oats and peanut butter and provided with cotton nesting material. Mice caught were marked with a combination ear-punch and toe-clip system so as to be individually recognizable when recaptured. Each animal was released

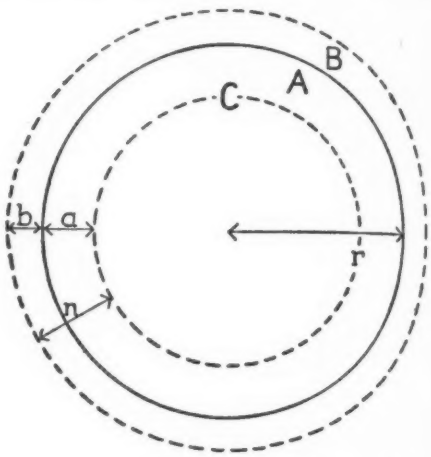

Fig. 1. Calculation of buffer margin for determining a small mammal population. *C*, area trapped; *A*, marginal area within trapped area; *B*, marginal area outside trapped area; *n*, mean diameter of range; *a*, width of inner rim; *b*, width of outer rim; *r*, radius of trapped area.

[1] Help by two members of Civilian Public Service Camp No. 34 is gratefully acknowledged, Clyde Vance in all field work and James Cope during the live-trapping. Mrs. K. C. Tabb made the maps (Figs. 2, 3).

where it was trapped. The live trapping continued for seven nights, September 4 to 10.

SNAP TRAPPING

In the snap-trapping method, as currently used, a quadrat up to one acre in size is trapped with a saturation number of traps for three successive nights and the results expressed directly as per acre figures. See especially Bole (1939) for discussion and application of this method. On September 11 a circular area of one acre was marked off in the center of the larger area, and 200 snap-traps distributed uniformly over the plot. The traps were baited with rolled oats and peanut butter and placed in saturation numbers to assure rapid capture of mice using the area. Trapping continued for three nights, September 11 to 13. Snap-trapping was continued after this date and the results on the later trapping will be presented elsewhere.

RESULTS

Results of the seven nights of live-trapping on the 17-acre area, followed by three nights of snap-trapping on the central 1-acre area, are shown in Figures 2 and 3. Enclosed sections indicate the areas in which the 139 individual adult *Peromyscus* were taken during the live-trapping. Actual sites of capture are spotted in. These areas are not to be interpreted as actual home ranges in the sense used by various authors (Burt, 1940; Dice, 1938, 1941; and Blair, 1940 a–d, 1941, 1942), but show merely the region in which each animal was actually trapped in the course of the experiment. The problem of home ranges is a separate and highly complex problem, not discussed in this paper.

On the basis of the live-trapping data, the density of adult *Peromyscus* is shown to be between six and seven per acre. The method of calculation is described in detail beyond.

All 23 adult mice taken during the 3-day snap-trap period had previously been taken in the live-trap period. The areas in which they were caught during live-trapping are shaded in on the maps, with an indication as to which of the three days of snap-trapping resulted in their capture in the central acre.

On the basis of these snap-trapping results the density of adult *Peromyscus* would be calculated, according to the standard procedure, to be 23 per acre.

It is evident that the snap-trapping took all animals normally using the area, and that the ranges of these animals unquestionably included an area several times larger than that of the central acre alone. *Hence, a per-acre figure based on the three day snap-trap catch on a single acre would be exaggerated by three to four times.*

ANALYSIS OF LIVE-TRAPPING DATA

Effectiveness.—During a live-trapping period it is assumed that all animals using the trapped area will be caught, marked, and released. The trap spacing and trapping methods were adequate to accomplish this as is clearly shown in the snap-trapping period when no unmarked adults were taken. At the time this report is written, continuous snap-trapping in the central acre for 35 days resulted in the capture of 54 adult *Peromyscus*, all of which had been

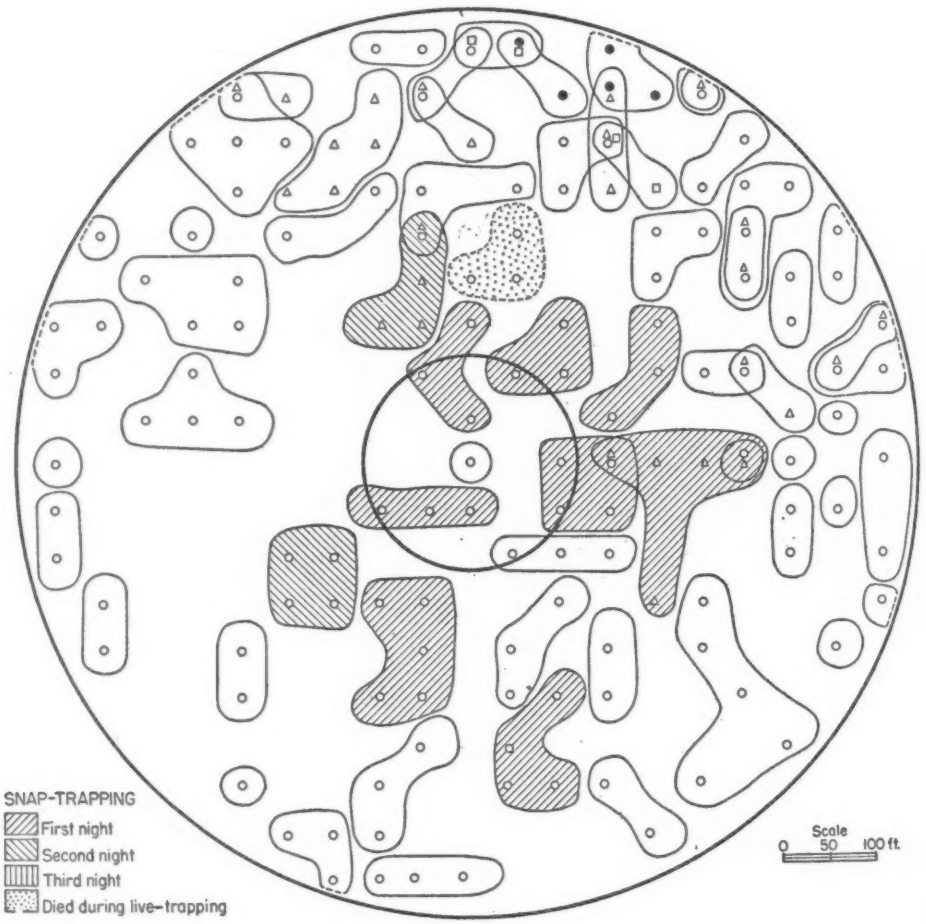

Fig. 2. Map of 17-acre trapping area (outer circle) showing the movements of 64 adult female *Peromyscus* taken during a 7-night live-trapping period. Actual sites of capture are spotted in. (These movements are not to be interpreted as true home-ranges.)

The central circular area is one acre in size; animals taken therein during three nights of snap-trapping are indicated by shading (no females taken during third night). The animal indicated in exact center of the area was taken only once, the first day of live-trapping. The other animal whose range is unshaded but touches the central acre, was taken each of the first three nights of live-trapping but not thereafter. Neither of them was taken after 35 consecutive days of snap-trapping and both were presumed to have left the area before snap-trapping began.

previously marked during the live-trapping.

The validity of the methods is likewise, though more indirectly, indicated by the fact that new animals were largely restricted to the peripheral traps after the first three nights of live-trapping (Table 1).

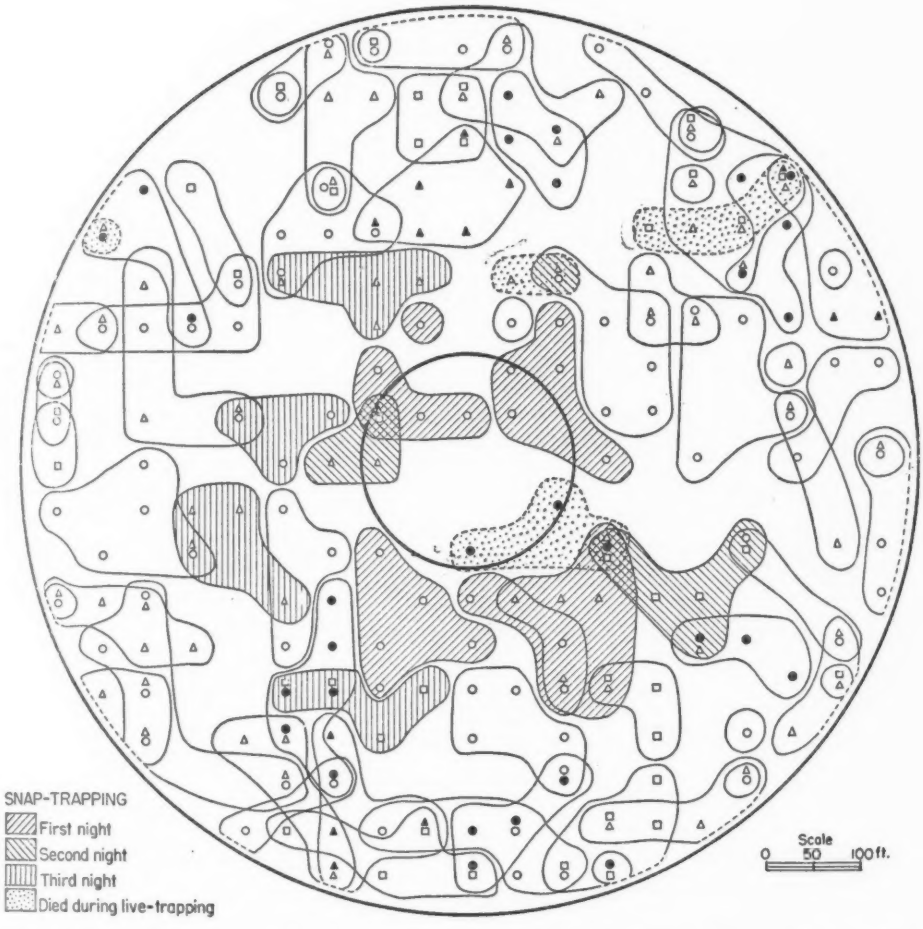

Fig. 3. Map of 17-acre trapping area (outer circle) showing the movements of 75 adult male *Peromyscus* taken during a 7-night live-trapping period. Actual sites of capture are spotted in. (These movements are not to be interpreted as true home-ranges.) The central circular area is one acre in size; animals taken therein during three nights of snap-trapping are indicated by shading.

The fact that the movements of individual animals during the trapping period are sufficient to enclose the area covered by several traps is also an indication of the adequacy of trap spacing. This supports the reliability of spacing and methods of Burt (1940) and others who have employed similar techniques.

Population calculation.—For the present study, in which an extensive area in the midst of similar habitat was trapped, a relatively simple and dependable method of estimating animal numbers, based directly on trapping data, can be employed. A reasonably accurate per-acre figure can be obtained as follows, males and females

considered separately.

In the course of the live-trapping 75 adult males were captured, marked, and released on the 17 acres.

The average maximum distance between traps in which individuals were captured during the 7-day trapping period is calculated for all animals taken four or more times. The distance of average maximum movement did not vary appreciably after four captures as shown in Table 2.

Thus, 146 feet is taken for the average maximum movement of the males. Roughly one-half of this distance, 75 feet, is used as the width of a buffer strip around the inside of the edge of the 17-acre study area. The population estimate is made for the 12.3-acre central area remaining after subtraction of the 75-foot marginal strip.

The animals taken in this central area numbered 52; those taken in the central area and also in the buffer strip numbered 21. Since 21 animals were shared between the central area and the buffer strip, one-half this number is allocated to the central area for calculation. The per-acre density figured on this basis (41.5 mice: 12.3 acres) is 3.4 adult males per acre.

In the live-trapping, 64 adult female deer mice were caught on the study area. The average maximum distance of movement by them was 93 feet, hence a 50-foot buffer strip was assumed. In the remaining central circle of 13.8 acres, 51 females were trapped. Thirteen of these were shared between the buffer strip and the central area. The per-acre density thus calculated (44.5 mice: 13.8 acres) is 3.2 adult females per acre.

TABLE 1.—RESULTS OF LIVE-TRAPPING PEROMYSCUS.

Trap night	Repeats	New animals in outer row of traps	All other new animals	Total new animals
1	0	21	60	81
2	59	8	23	31
3	72	7	4	11
4	76	4	2	6
5	65	4	0	4
6	62	4	0	4
7	59	3	1	4

TABLE 2.—AVERAGE MOVEMENT OF PEROMYSCUS.

Repeat captures	Males		Females	
	Number of mice	Average movement (feet)	Number of mice	Average movement (feet)
3 to 7	53	140.7	45	86.8
4 to 7	47	146.1	33	93.1
5 to 7	34	147.2	20	93.9
6 to 7	27	142.9	10	90.8

The total population therefore was estimated to be between 6 and 7 adult *Peromyscus* per acre.

Juveniles.—During the live-trapping period most of the females were either pregnant or nursing, and very small young soon began to be taken in the traps. The juveniles are not included in any of the calculations. The data for them are summarized in Table 3.

TABLE 3.—JUVENILE PEROMYSCUS CAPTURED.

Date	*Number caught*	*Condition*
LIVE TRAPPING		
September 6	1	Recently out of nest
September 7	5	Recently out of nest
September 8	1	Recently out of nest
September 9	2	Recently out of nest
SNAP TRAPPING		
September 12	2	Both marked
September 13	2	One marked, one new
September 14	2	Both new

Other interpretations of data.—When live-trapping is conducted on a quadrat, all of the animals taken will not be of those restricted to the quadrat. Many, especially those at the margins, will include areas outside the quadrat in their normal movements. To compute the population size by dividing the number of animals taken by the number of acres trapped would result in an exaggerated figure.

This will be true in trapping a quadrat in the midst of land of similar type. If the trapped area is surrounded by territory providing a barrier to the species being studied, as in Burt's extensive studies of *Peromyscus leucopus* in Michigan, direct computation can be made. In the present study, the area trapped was sufficiently large that the marginal area could be treated as a buffer strip, and the computations thus based directly on trapping data.

In cases where such direct methods cannot be used, some other allowance must be made for those animals which range outside the trapped quadrat. In an area of continuous habitat a true per-acre figure could be obtained by adding the area of a rim of x width to the periphery of the trapped area to obtain an areal figure for calculations. Dice (1938), Burt (1940), and Blair (1941a) recommended that the width of the rim should be one-half the average width of a home range. One difficulty in this method is determination of the true home range. Dice (1938; 1941) has pointed out that the calculation of home ranges by the method proposed by him is based on the assumption that all parts of a habitat are occupied by mice with contiguous but not overlapping ranges. He states, however, that in practice these conditions are seldom met. In the present study it was found that the individual ranges did overlap and that parts of the habitat did not seem to be occupied.

In consideration of the fluctuating nature of populations, it is plain that data for a population estimate should be gathered in as short a time as consistent with reliable results. Gathering data on home ranges over an extended time period and then applying the results to calculation of populations of animals based on a short trapping period is open to question. For any given trapping period, however, the movements of the animals during the trapping period can be demonstrated. These movements ordinarily cannot be considered to be home ranges, but

the actual movements of the animals in the given area in the given period are the item of importance in attempting to derive figures on populations.

Also, if the area of a marginal portion of a width related to the average diameter of the range of the animals (either home ranges or actual movement during the period of calculation) is to be added to the area of the trapped plot to compute the per-acre density, the width of this rim should not be one-half the width of a range, because this practice would produce progressively greater areal inaccuracies with increase in size of the area studied. The result would be to yield rapidly decreasing per-acre figures with increase in the size of the area considered.

It would be better to divide the mean range (or movement) diameter between a width inside the trapped area and a width outside the trapped area in such a way that the two rims would have equal areas. Thus, if using a circular area (Fig. 1) Area A should equal area B, and $a+b$ should equal the mean diameter of the range. If n (mean diameter of range) and r (radius of trapped area) are known, then a and b can be calculated in terms of r and n by the following formulas:

$$b=n-a \qquad (1)$$

$$a=\frac{(2r+n)-\sqrt{4r^2-n^2}}{2} \qquad (2)$$

A circle of radius $r+b$ can then be used as the areal unit on which to base population estimations.

Data from the present study can be used as an example of this method. For comparison with the method of estimation presented in the previous section and to eliminate the possible error in using marginal trap data, the computation is made on the trap plot of 13.8 acres for females and 12.3 acres for the males. To apply the formula it is necessary to know the values of r and n. The radius of the study area, r is taken to be 438 feet for females, 413 feet for males. The average diameter of movement, n is roughly 150 feet for males and 100 feet for females. When the formula is solved the value of the rim b to be added is 68.15 feet for males and 47.15 feet for females. Use of these figures for population calculations gives estimates of 3.1 adult males and 3.0 adult females per acre. The principal sources of error in this method of calculation are brought out in the discussion above. Nevertheless, these figures are very close to those derived by the more direct method.

SNAP-TRAPPING

In population estimates made by snap-trapping, the conclusions have customarily been based on three nights of trapping. The catch of animals after three nights usually falls off sharply and this has been taken as evidence that the catch of the three nights includes only those animals resident on the area, and that the catch after that period results from drift of animals into the area from outside. Bole (1939) discusses this problem and on the basis of the sharp decline in the number of animals taken after the third night in most of his extensive trapping concludes that "a three-day trapping limit should be set, as the resident population is practically exhausted in this time."

The size of the plot used in snap-trap censuses has varied widely. Bole gives a

comprehensive analysis and discussion of the snap-trap quadrat method. He compared the catch in quadrats of 10-meter, 50-foot, and 150-foot squares, and found a marked decrease in the results with each succeeding larger quadrat. The 150-foot quadrat, which is the largest he used, comprises approximately one-half an acre.

For the present study a 1-acre area was chosen to conform with the present trend in snap trap work. A circular area of this size is used by Dr. S. Charles Kendeigh in censuses at the University of Illinois, and the "acre-trap" is in use by Donald A. Spencer and his associates for the censusing of *Microtus*.

The most complete study and use of the snap trap method has been made by Bole (1939). Others who have recently published population density figures based on this method include Aldrich (1943), Dambach (1944), Gray (1943), Odum (1944), and Williams (1936). Storer, Evans, and Palmer (1944) trapped out 0.78 acre plots, using periods longer than three days, and based their per-acre figures on these data. However, after live-trapping on the same area they concluded that the snap-trap results were inaccurate for population figures.

When populations are calculated from a snap-trap quadrat and numbers obtained in three nights are used uncorrected, it has apparently been assumed that the animals taken in three nights are all those which use the area and that these animals are confined to the area or else that deviations are in some way compensatory.

Exaggeration of population figures will result whenever the normal movements of an animal include territory outside the trapped quadrat. This will always be true regardless of size of quadrat, but becomes increasingly more serious as the size of the quadrat in relation to the range of the animal becomes smaller. Bole (1939) demonstrated by comparative experiments the unreliability of quadrats less than one-half acre in area. The present experiment indicates that the exaggeration is very great even on a 1-acre plot.

Another source of error is in the removal of animals from the quadrat. Neighboring individuals appear to extend their ranges rapidly upon removal of other animals, and the capture of some of these "neighbors" further exaggerates the population numbers obtained. Some workers have used data from trapping periods of more than three days, and their results are open to even greater question.

On the basis of results of this study, and in light of the above discussion, snap-trap censuses, as generally made, do not produce accurate population figures.

Snap-trapping for the comparison of populations.—The snap-trap method or modifications of that method have possibilities for development as a good *relative* means of measuring populations. Use of relative index figures rather than absolute per-acre estimates in studying the differences and fluctuations of small mammal populations would seem to be more reliable and accurate. Certainly such relative appraisals are more easily obtainable than attempts to obtain true per-acre figures, which are laborious and often unreliable This is the belief of Dice (1941), and evidently also of Evans (1942), because the latter's comprehensive work was based on a method

(live-trapping) giving relative information.

A recent paper making use of the snap-trap quadrat as a relative method is that of Koestner (1944) who uses a 3-day population index to express his results.

SUMMARY

The *Peromyscus leucopus* on a 17-acre study area were live-trapped, marked, and released over a seven-day period. On the three following nights intensive snap-trapping was done on the central acre of the study plot.

The animals caught by snap traps in the central acre represented the population of the central acre and several surrounding acres. By the currently accepted methods of interpreting snap-trap data, the population per acre would be considered to be 23 adults.

The live-trap data show that the true population was between six and seven adults per acre. Modern methods of live-trapping are shown to be valid for population studies.

Two methods are presented for the conversion of live-trap data into per acre figures.

Errors involved in the current use of snap-trap data are discussed and snap-trap methods are shown to be invalid for determining actual population numbers.

It should be practical to use a snap-trap quadrat technique to obtain a relative measure or index figure for small mammal populations.

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COPULATION IN THE PORCUPINE

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Taylor (1935), in his comprehensive paper on "Ecology and life history of the porcupine (*Erethizon epixanthum*)," brings together in one page on "manner of copulation," the scant information available on this subject and says, "available accounts of the actual mating process do not agree." Struthers (1928) witnessed the process once in the laboratory, and few persons have seen it in the wild. The following observations on *Erethizon d. dorsatum* are recorded because of the lack of detailed information.

Of the animals used, female no. 1 ("Maudie," 12.5 lbs., 8 yrs. old) and male no. 1 ("Old Dad," 20.25 lbs., 9 yrs. old) were obtained from Allegany State Park, New York, through cooperation of the Allegany State Park Commission. They now have been in the laboratory for several years. Female no. 2 ("Nightie," 16 lbs.), black and heavily-haired, was received in 1942 from Poughkeepsie, New York, through Donald Spencer of the U. S. Fish and Wildlife Service.

FIRST CASE

The female, "Maudie" (Pl. 12, A), bred and produced one young each in 1941, 1943, and 1944 (Shadle and Ploss, 1943), but in none of these cases was the mating observed. For some time she had been in one half of a large wire cage; the male ("Old Dad"), used in previous matings, occupied the other half. After showing some signs of rut for three or four weeks, she was at the peak of this condition on November 18, 1944.

For several days the female had been rather quiet, had eaten very little food, and remained on the side of her cage toward the male. She frequently climbed up on the wire, where her genitals could be nosed by the male and these olfactory tests usually produced more or less sexual stimulation of the male. His excitement was evidenced by (1) "singing" (whining in a low tone); (2) doing a "three-legged walk" while holding the left fore paw on his genitals; (3) rubbing his genitals on the timbers of the cage, or on the food and water crocks; (4) rubbing the side of his nose against objects; and (5) holding a long stick in his fore paws and straddling it as a child does a broom-stick. The stick was held so that his genitals were stimulated by the contact, and the wood soon accumulated odor from the urine and glandular secretions absorbed. In conse-

quence, it was a source of sexual stimulation to both male and female.

At 11:15 A.M. the female, at the peak of heat, was placed on the floor of the male's cage. As he moved toward her, she stood perfectly still, raised her tail nearly upright, and presented her genitals directly (Pl. 12, B). He nosed her vulva and she raised her tail still higher, backing toward him in a breeding posture. In two or three minutes during which his sexual excitement increased to the necessary level, the female, her genitals fully exposed, continued to back against his nose and head.

When the male attained the stage of excitation to attempt mating, the female stood on all fours with her tail about 10 to 15 degrees from perpendicular; then the male reared on his hind legs and tail, his penis fully erected, walked up behind her (Pl. 12, C), and almost immediately made sexual contact (Pl. 12, D). The quills on both porcupines were relaxed and, with the female's tail raised, no spines interfered with copulation. The bristle-covered ventral side of the female's tail came against the bristle-covered belly of the male, and her tail thus was pushed forward out of the way.

The male did not grasp the female, but stood erect with his fore limbs held well above her body, except when one limb seemed to rest lightly on the distal third of her tail, which at times, was in an S-shape above her back (Pl. 12, B).

The female usually stood still with her head lowered; during contact she pushed actively against the thrusts of the male. His rapid, vigorous thrusts were of the usual nature, but produced mainly by alternately flexing and straightening his knees. A secondary factor in the thrust was the action of his tail. In the erect position, the tail and hind legs formed a tripod support, but in the copulatory action, the tail alternately bowed and straightened.

Vigorous sexual union continued for one to five minutes. When the male broke away, even for a few seconds, the female would immediately attempt to reestablish contact, either by backing up to him as he stood erect, or by changing to a more preferable position. The animals were left together for 15 minutes, and then separated so that photographs might be made later.

At 1:30 P.M. the two porcupines were again placed together; they soon developed sexual urge and again were ready for copulation. Sexual contact was made repeatedly, and for two to four minutes each time. There then was no lack of vigor or aggressiveness on the part of either as compared to events during the morning.

For a time, the desire of the female seemed almost insatiable. There were repeated copulations, and after each, the female sought to repeat. After 20 minutes of very active effort, the male was fairly exhausted, but the female remained aggressive (Pl. 12, F). This male was then returned to his cage and, in turn, two other males were brought in and placed with the female, but neither showed any interest; they had not been associated with her recently. When ignored by the albino male no. 2, "Pinkie," the female reacted toward him as a male usually would react to a female.

While this female was with each of the other two males, a vaginal plug protruded from her vulva. It was about one-half inch long and nearly the same

in diameter, and of a bluish-white, starchy appearance, (Pl. 12, E).

At 2:20 P.M. "Maudie" and "Dad"; were again placed together in her cage. They were in sexual contact from 2:30 to 2:35 P.M., after which they were separated; the male was sexually exhausted. At 4:30 P.M. the two animals were again brought together, but the female had already become quite sensitive about the genitals and resented advances by the male. She had been aggressively receptive at 2:30 P.M., but two hours later was not, and struck with her tail every time the male nosed her genitals.

SECOND CASE

On November 26, 1944, at 3:55 P.M., female no. 2 ("Nightie") was at the peak of rut. She was first placed with "Old Dad," the oldest and most aggressive male. Copulation was rather prompt and a repetition of the process as described. This 30-month old female was much more active than the 8-year old "Maudie". The younger female also was more excited and emitted an almost continual grunting whine except during actual coition. The male again stood erect on his hind legs and tail and did not use his fore limbs to hold the female. He made eight or more contacts within 20 minutes, then seemed completely exhausted. Later he made several unsuccessful trials.

During the next two hours, three other males were tried with no success. Within four hours after the original mating, this second female was past the stage of accepting a male.

"Old Dad" had been kept in a cage between these two females and so was familiar with and willing to accept both of them. A younger male, "Johnnie" (43 months old), was kept in a cage between female no. 2 and another female, but showed little interest in mating with either. The albino male also exhibited little interest in either one. Although the females were at the peak of heat, lack of sufficient previous close association with these two males made them unacceptable to the latter.

DISCUSSION

In both cases here described, the approach of the male was similar to that described by Struthers (1928), but in neither did the male use his fore limbs to hold the female. The female described by Struthers held her tail "sharply to one side," while both of our females held theirs forward and directly above the middle of the back.

Taylor (1935) quotes a trapper who said "he once saw a pair of porcupines copulate, standing belly to belly." This obviously was no copulation, the position of the animals being typical of a courting procedure (Shadle, Smelzer and Metz, 1946, in press). Such behavior may precede copulation by a few days to many days, and may occur many times before a female reaches the peak of heat and is ready for copulation. A knowledge of the position of the genitals in the two sexes shows that it would be impossible for porcupines to copulate in a standing position "belly to belly."

SUMMARY

Two of three observed laboratory copulations of Canadian porcupines occurred during November 1944, at the University of Buffalo, and afforded the first photographs of the process.

A female at peak of heat will accept any male, is very aggressive sexually, and remains so until two to four hours after coition. A copulation plug is formed within a few minutes.

Preliminary association with the females seems necessary for the male. The male approached from rear, standing up on his hind legs and tail, but did not use his fore limbs to hold the female. The sexual contact lasted two to five minutes.

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EVALUATING RAT BAITS BY FIELD ACCEPTANCE TRIALS ON GUAM[1]

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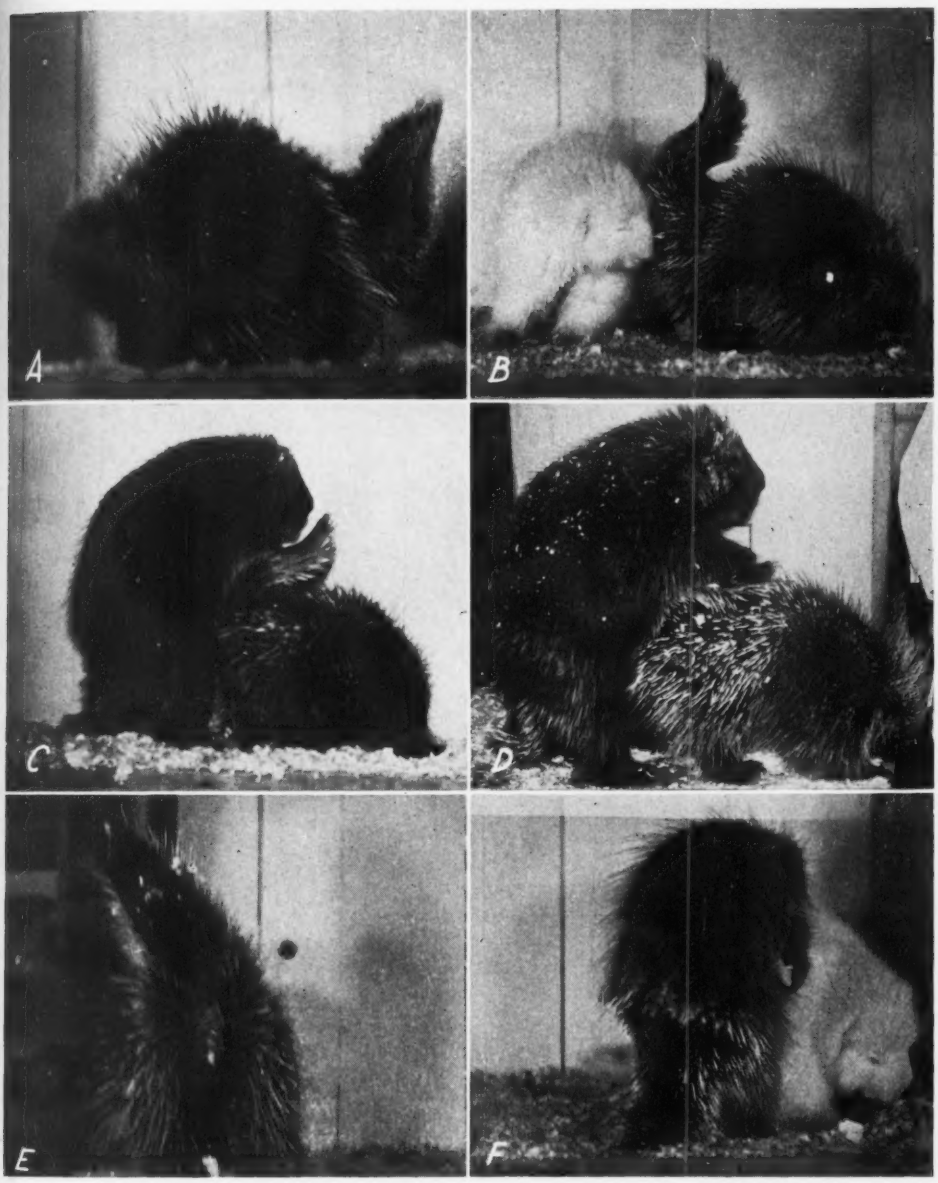
Rodent control has been a measure for prevention of epidemic disease in the armed forces. Rodent control officers (mostly former wildlife biologists) have been confronted overseas with little known species and many problems that required investigation. One of these has been the choice of bait materials for poison campaigns and bait acceptance trials have been the logical solution for this problem. Trials were initiated on Guam early in 1945 when an island-wide rodent control program was organized. A prebaiting-feeder station technique was universally promoted for the poisoning of rats, and the trials were concerned with choosing baits suitable for use in feeder stations.

The adaptation of available quartermaster supplies or local produce to control programs was imperative. Often conventional supplies were unavailable while some particular item of food not ordinarily considered rat bait was overabundant. Selection of the most acceptable cereals and the most acceptable oils and final determination of the most acceptable combinations of oil and cereal were all of fundamental concern.

This paper presents a method for trial of baits, its uses and limitations. The specific results are applicable only to local conditions, but the method should serve in similar cases anywhere.

Two species of rats were found on Guam. *Rattus exulans*, the small Polynesian rat of the *concolor* group was irregularly distributed all over the island.

[1] This work was done while both authors were serving as Lieut. (jg) USNR; the manuscript has been passed for publication by the Division of Publications, Bureau of Medicine and Surgery, U. S. Navy Department. Lieut. T. B. Murray, USNR (of Fish and Wildlife Service), gave helpful advice during the study.



Copulation in the porcupine. *A*. Female no. 1 at peak of heat in typical receptive position; tail held upright and genital organs bared (compare Fig. *E*). *B*. Albino male, no. 2, in typical olfactory test of the genitals of female; tail of latter in S-shape over her back, exposing her genitals to contact. *C*. Male no. 1 standing almost erect on hind legs and tail and approaching from rear and slightly to left of the female; his fore paws do not touch the female. *D*. Male has established sexual contact, standing up directly behind the female, his paws resting lightly on her tail, which is laid forward over middle of back. Again his paws do not touch or grasp her sides. The white flecks are shavings from the floor. *E*. Rear view of female, showing position of tail after copulation. The whitish vaginal plug protrudes from the vagina. *F*. Having mated several times with Male no. 1, (then sexually exhausted), the female seeks further contact with Male no. 2. He showed no interest, and she immediately assumed toward him the reaction of a male toward a female. Photographs by Drs. William A. Ploss and James W. Johnston, Jr.

Mt. Macajana area, Island of Guam. *A*. Interior of bait trial station. Five such stations were used as a unit for each trial. *B*. Typical local landscape, supporting heavy rat population.

It seemed to be more numerous in the vicinity of cultivated or formerly cultivated land. The species was always in a minority position and in no place was found as a pure population. Some rat populations were found free of this rat.

Rattus rattus (*neglectus-diardii* section according to the U. S. National Museum) was the principal species of concern, being common all over Guam. In many places its numbers constituted definite threats to security from epidemic disease, although no rat-borne diseases were known to occur on the island.

Both species live in no particular relationship to the presence or absence of human habitation (Pl. 13B). As characteristic of this genus, however, both species were opportunists and were quick to take advantage of food and shelter available in native establishments and the multitudinous military activities on the island.

EQUIPMENT

Each bait trial used a unit consisting of five feeder stations. Each station was equipped with eight feed dishes arranged in a circle, accommodating four, four-ounce samples of bait, approximately divided into two-ounces portions (Pl. 13A). Opposite feed dishes contained the two portions of a bait. The center piece was so constructed that it could be rotated and taken out for cleaning. Large-headed tacks in the periphery of the center piece fitted into notches of the feeder dishes to hold them in position. Each station was constructed with a removable water-proof cover and had four $2\frac{1}{2} \times 3$-inch entrances, for the rats at floor level, one at each corner. The cover was so fitted that rats could enter or leave at either end of the top of the station. A station, screened against rats, was used as a control in conjunction with each unit.

METHODS

A location supporting a comparatively heavy population of rats was selected for each trial, although acceptance with some baits seemed to indicate otherwise. The five stations of a unit were placed in likely cover and at distances of 30 to 200 yards apart. Thus all stations of a unit were kept well within the weekly cruising radius of an individual rat which was arbitrarily considered to be 150 yards. The baits were rotated 45 degrees clockwise each day in each feeder station of the unit. Thus each bait occupied the same relative position in each of the five stations but a new position in the station each day. Each trial was run four or five days, depending somewhat upon the degree of patronization of the stations. Maximum use of the stations by the rats ordinarily was reached on the fourth day. Daily total consumption began to level off at this time, especially if the baits under trial were highly acceptable. The baits remaining in the stations were weighed daily to the nearest quarter-ounce, then discarded.

The day following the termination of each trial, 10 wooden-base rat traps baited with fresh copra were set in and around each station, making 50 traps per unit of five stations. Thus a proportion of the rodents whose food preferences had been indicated in the trial were caught. Records were kept of species, sex, age, breeding condition, and general nutrition.

SELECTION AND PREPARATION OF BAITS

Selection of high preference baits was considered imperative for use in the intensive control program in progress. Since baits with high acceptability often vary in control value with different populations and in the same population at different times, it was considered necessary to ascertain three or four highly acceptable combinations of cereal and oil so that bait rotation could be practiced. Only foods of probable value were selected for testing since time and manpower limited the number of trials possible. Each trial furnished pertinent information concerning specific current problems.

It has been repeatedly observed that wise selection tends toward economy of materials, manpower, and transportation. Furthermore, better baits have been useful in overcoming the difficulties of controlling "wise" populations with previous poison experience or those adjusted to peculiar environmental conditions such as rats living in the presence of abundant preferred foods, a common circumstance on Pacific islands.

Baits used in the trials were of those food materials obtainable from quartermaster supplies or from native sources. Available cereals were farina (white, processed wheat cereal), rolled oats, bread, "C" biscuits,[2] and whole-wheat cereal. The principal available oils were corn oil (Mazola), bacon grease, peanut butter, and copra.

Foods used in the trials were carefully weighed and mixed in exact proportions. Enough bait was mixed before the trial started to last five days. An exception was made for bait flavored with canned salmon because it tended to spoil unless freshly made each day. Since most oily baits apparently were

TABLE 1.—BAIT-ACCEPTANCE TRIALS—TOTAL OUNCES OF EACH BAIT CONSUMED.

Trial	*Days in Trial*	Baits (see Figs. 1–3 for materials)				*Total bait taken*
		A	B	C	D	
1a	5	19.25	26.25	8.75	7.75	62.00
1b	4	15.25	11.75	3.50	3.50	34.00
1c	4	28.00	44.75	28.25	20.50	121.50
3	4	9.75	12.75	18.50	8.25	49.25
7a	3	10.00	15.00	7.25	20.50	52.75
7b	3	9.50	17.25	9.25	14.75	50.75
8	5	5.00	1.75	11.00	14.00	31.75
9	5	12.75	14.25	16.50	10.25	53.75
10	4	1.75	14.25	22.50	9.00	47.50
11	4	11.25	10.50	19.50	16.25	57.50
17	4	9.25	5.00	4.50	13.00	31.75
18	4	14.25	12.50	8.75	21.00	56.50
19a	4	2.75	2.75	1.50	1.75	8.75
19b	4	6.25	3.50	2.50	3.75	16.00
19c	4	14.25	13.25	8.50	6.75	42.75
19d	4	13.75	9.25	7.25	3.50	33.75

[2] Biscuit (hard bread) type "C" Ration SQ. Loose Wiles Biscuit Company, Dallas, Texas.

more acceptable to rodents three to five days after mixing than when fresh, such aging was practiced.

TREATMENT OF DATA

This experiment was designed to utilize the advantages of the analysis of variance. Under statistical control were the variation between days and the variation between baits. Variables not under statistical control were those dealing with meteorological conditions, number of rats visiting a station or unit, disturbance of the whole rat population by external influences, and previous conditioning of rats as to food and wariness. The results from feeder stations varied so that their use as the basic unit of data was contraindicated. Since there was no controlled randomization of the variability between stations, different numbers of rats probably ate at different stations on different days. Acceptance from units as a whole increased fairly uniformly in all but a few trials, giving a positive regression between ounces of bait and days. As the rats became accustomed to a unit they either ate more, or more rats visited the unit, or both such changes occurred.

In analysis of these data it was highly important that the sampling distribution be known and a compensation made if necessary. It was theoretically held that each sample of bait was a portion of an unlimited population of bait, but all of one bait could have been eaten and the greatest possible difference between two baits was one not eaten at all and another completely devoured. From this viewpoint a proportion was indicated. The variance of a single bait for a single day is thus described by the binomial $(p+q)^n$, p representing the proportion eaten, q the proportion not eaten, and n the number of quarter ounces. The variance is pq/n, and the standard deviation is $\sqrt{pq/n}$. The resulting curves are skewed unless p equals 50 per cent, and there-

TABLE 2.—VARIANCES AND F-TESTS OF SIGNIFICANCE OF BAIT-ACCEPTANCE TRIALS.

	Degrees of Freedom			*Variance due to*			*F-tests*	
Trial	*Bait*	*Days*	*Inter-action*	*Bait*	*Days*	*Inter-action*	*Bait vs. Inter.*	*Days vs. Inter.*
1a	3	4	12	692.0	379.6	16.9	40.9[b]	22.4[b]
1b	3	3	9	195.8	38.7	29.6	6.6[b]	1.3
1c	3	3	9	237.7	123.2	53.8	4.4[a]	2.3
3	3	3	9	90.7	140.8	16.0	5.7[a]	8.8[b]
7a	3	2	6	412.6	90.9	12.6	32.7[b]	7.2[a]
7b	3	2	6	185.5	116.0	31.9	5.8[a]	3.6
8	3	4	12	500.2	24.7	41.6	12.0[b]	0.6
9	3	4	12	76.0	212.5	21.0	3.6[a]	10.1[b]
10	3	3	9	425.7	155.5	24.6	17.3[b]	6.3[a]
11	3	3	9	56.9	62.2	28.3	2.0	2.2
17	3	3	9	87.3	12.4	9.1	9.6[b]	1.4
18	3	3	9	96.2	24.4	30.1	3.2	0.8
19a	3	3	9	22.2	27.6	30.4	0.7	0.9
19b	3	3	9	26.6	41.0	9.2	2.9	4.4[a]
19c	3	3	9	44.9	143.4	22.5	2.0	6.4[a]
19d	3	3	9	96.4	105.6	33.7	2.9	3.1

[a] Exceeds 5% level of significance.
[b] Exceeds 1% level of significance.

fore the data do not fit a normal curve. A conversion for this type of data has been devised by Bliss and expounded by Snedechor (Statistical methods, 1940: 380). The percentage was converted to degrees where

$$\text{angle} = \text{arc sine } \sqrt{\text{per cent.}}$$

Data thus converted approach normality. This technique has been applied to these data.

Analysis of variance was carried out on each test, using bait and days as the two variables. The bait×days interaction was used as the best estimate of error. The variances from the complete set of tests were compared by the chi-square method and found homogeneous. The difference between two means necessary for significance (at the 5% level) was calculated from the error term for each test, and the bait means for each test were compared.

The ultimate object of this analysis was to evaluate baits upon their relative merits. It would have been incorrect to say "Bait A is twice as good as bait B." An inference would have been connoted that twice as much of bait A was consumed. That would not necessarily have been a significant difference; on the other hand, it might have been several times the necessary difference for significance. These data accordingly have been evaluated upon the level of significance, using plain rolled oats as a standard.

The results are diagramed in Figures 1–3. Rolled oats, the standard, was represented by the zero point. A bait which was just (5% level) significantly better was 1, if similarly poorer it was −1. The area below significance is hatched, that beyond is solid. Any difference between bars (within trials) as great as 1 unit indicates a significant (5% level) difference.

TABLE 3.—ANALYSES OF THREE TRIALS; COMBINED DATA.

Source of variation	*Degrees of freedom*	*Sum of squares*	*Variance (mean square)*	*F*
TRIAL 7				
Total	23	2479.57		
Baits	3	1546.98	515.66	12.12[b]
Tests (Replications)	1	4.38	4.38	0.10
Error (Within Subclasses)	16	680.85	42.55	
Bait-test Interaction	3	247.35	82.45	1.94
TRIAL 1				
Total	51	7647.77		
Baits	3	1806.96	602.32	12.32[b]
Tests	2	3618.17	1809.08	36.99[b]
Error	40	1916.38	48.91	
Interaction	6	306.43	51.07	1.04
TRIAL 19				
Total	63	3878.80		
Baits	3	422.36	140.79	3.72[a]
Tests	3	1492.92	497.64	13.16[b]
Error	48	1815.42	37.82	
Interaction	9	148.10	16.46	0.43

[a] Exceeds 5% level of significance.

[b] Exceeds 1% level of significance.

CEREAL TRIALS

Rolled oats was the cereal of choice in all trials, although the combination of whole wheat cereal and ground fresh

copra (4:1) was an acceptable bait (plus 1.05). Five tests (Fig. 1) were made with rolled oats in competition with other cereals including dry ground bread, whole-wheat cereal, farina, and ground "C" biscuits. In Trial 17 (without an oil) testing rolled oats, dry ground bread, ground "C" biscuits, and whole wheat, the rolled oats was significantly better than bread or whole-wheat and doubtfully significantly better than "C" biscuits. In one trial testing rolled oats, dry ground bread, and whole-wheat cereal in which ground fresh copra was mixed with each (4:1), rolled oats was not a significantly better cereal. In Trial 9 which compared rolled oats, whole-wheat cereal, and farina with ground fresh copra added to each (4:1), all copra baits were taken more heavily than rolled oats alone, and rolled oats and whole-wheat were both significantly better than the standard. In Trial 8 comparing rolled oats, whole-wheat cereal, and farina when mixed with peanut butter (6:1), rolled oats was the significantly better cereal, but the plain rolled oats standard had an even higher acceptance.

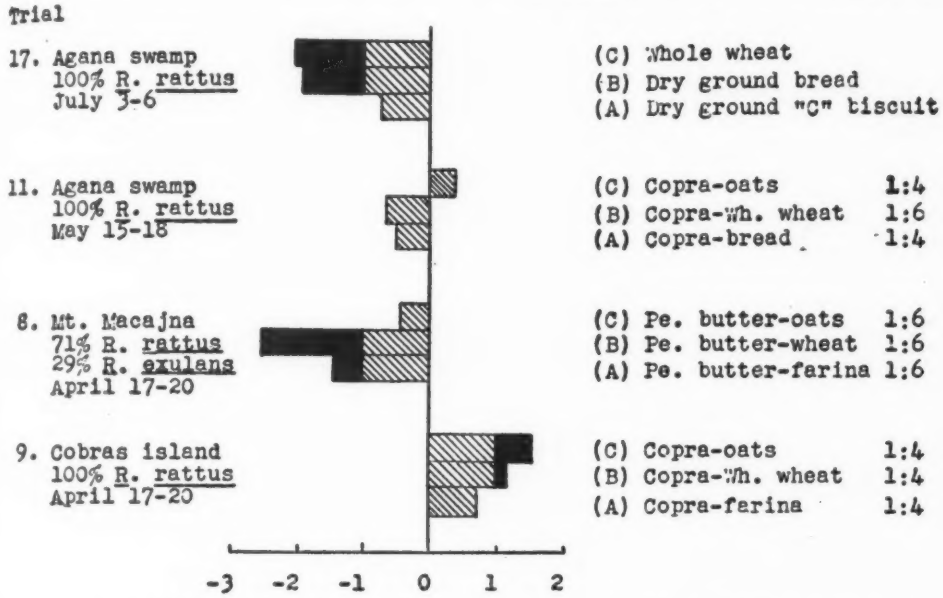


Fig. 1. Cereal trials for rat baits; rolled oats as a standard (0). Hatched areas represent less than significant differences. Note that good oils were inadequate to overcome aversion to poor cereals.

OIL BAIT TRIALS

Ground fresh copra was an outstanding choice as an adjuvant to cereals offered in trials (Fig. 2). Seven trials were made with rolled oats and copra or copra oil in competition with other oils and oily bases. Copra-rolled oats was significantly better than the standard rolled oats in all oil-choice trials. Copra oil with rolled oats was significantly better than rolled oats in two trials, but not in a third. Rolled oats with bacon grease

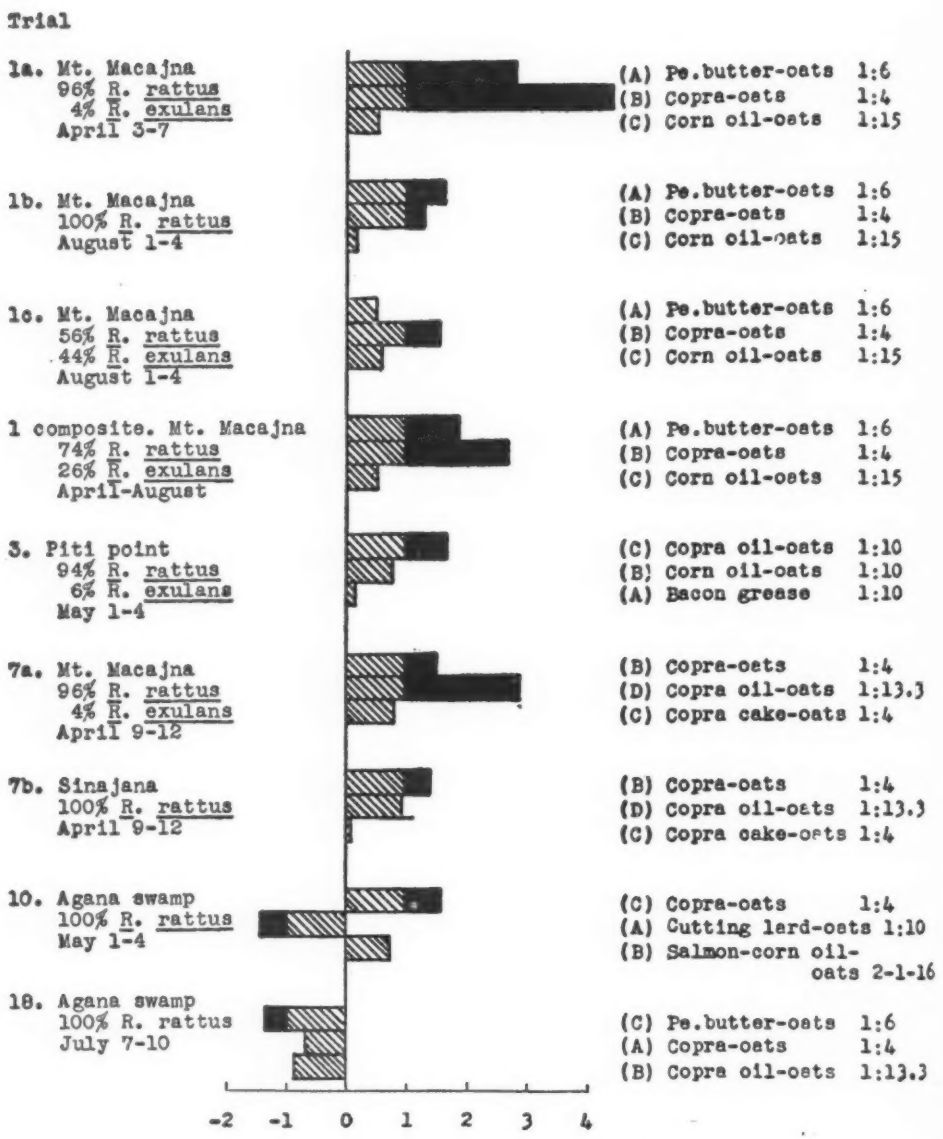


Fig. 2. Oil trials of rat baits; rolled oats as a standard (0). Hatched areas represent less than significant differences. Note the preponderance of preference shown for copra-rolled oats combinations.

or corn oil (Mazola) were better than the standard but not significantly so. Addition of salmon and corn oil was not significant. Copra cake (by-product of an oil extraction plant) was not inferior to the standard, but addition of cutting lard was significantly worse than rolled oats. The oil-adjuvant of choice was ground fresh copra; the oil extracted from copra and peanut butter were close seconds. Corn oil was not a significant improvement to dry rolled oats,

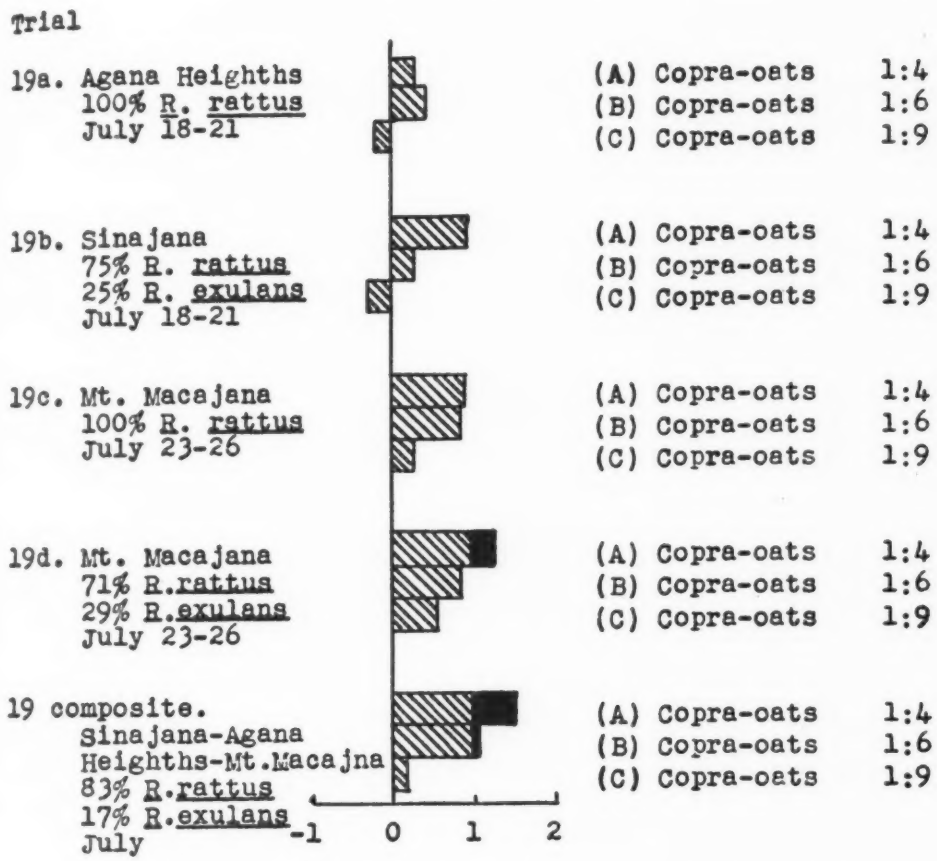


Fig. 3. Trials of copra and rolled oats combination in various concentrations as rat baits. Significance was enhanced by combining and analyzing four replicates.

but might be a permissible oil-adjuvant if the more preferable oils are not available. The other oils were contraindicated or, if used only justifiable as a carrier of poison particles.

OIL AND CEREAL COMBINATIONS

After the superiority of copra-rolled oats in combination had been demonstrated, it was desirable from the standpoint of economy of labor and materials to determine the most acceptable quantitative combination of the two. Four duplicate trials were performed on copra concentration using rolled oats as a standard (Fig. 3). In all cases the original copra-oats ratio of (1:4) was better, but in no case was this difference significant. An analysis of the four tests combined revealed that: (1) the relative standings of the baits in the four tests were not different; but (2) the relative take of baits on different days was significantly different. Since the result indicated an independence of days, the analysis was revised using days as an independent variable (Snedechor, 1940, p. 230). Both bait and tests exhibited significant differences, but their interaction was not significant (as indicated

in item 1, above). Comparison of the concentrations on this basis revealed that rolled oats-copra 4:1 and 6:1 were significantly better than rolled oats, but not significantly different as between these two concentrations.

CONCLUSIONS

Properly designed trials of bait acceptance will indicate the baits of choice for a number of contiguous rat populations living under essentially similar environmental conditions.

The trials reported here were designed without precedent and some alterations became necessary as information was gathered and faults in the technique were discovered. The uncontrolled variables in animal research of this type are numerous, and great caution is needed in design of experiments. From these trials several theories, principles, and substantiated evidence of facts have evolved.

A number of precautions are necessary in conducting such trials. First, a more or less naturally delimited population should be chosen. Within the habitat area of this population, the bait stations should be placed in spots that rats are most likely to visit. One trial should not follow another in the same area until the rats have become reacclimated to their usual food habits. In the one instance where this was done, plain rolled oats was significantly higher in acceptance than whole wheat or dry bread, and near significantly higher than "C" biscuit in the first trial (Trial 17) of four days. The second trial (Trial 18) followed immediately, using the three best baits, copra-rolled oats 1:4, copra oil-rolled oats 1:13.3, and peanut butter-rolled oats 1:6 with rolled oats as the standard. In this second trial of four days, plain rolled oats maintained nearly significant superiority over these baits. Examination of the results day by day showed that the other baits were gaining on oats, and eventually would have assumed their usual superiority.

Changes of relative superiority were noted in the trials as a whole. The results of the last two days of each test were compared with the complete tests. Save for a few exceptions, the last two days were less significant than the test as a whole, whether the bait in question was superior or inferior. In general, it seemed that the most selective discrimination was exhibited during the first two days of a trial. These early differences in baits probably were indicative of previous conditioning of the rats. On the other hand, better baits would assume, by the conditioning process, an established superiority which would enhance subsequent acceptance of a poisoned bait containing the same ingredients.

Another factor of great importance is to conduct several replicates of a trial. One more variable is added, but the degrees of freedom associated with error are increased, and an independent estimate of error is furnished, thus allowing a test of significance of the interaction of bait with one variable as well as testing the bait for significant differences. Such an analysis was made on three trials (Table 3). Trial 7 was replicated twice, Trial 1 was replicated three times and Trial 19 was replicated four times. Trial 1 tested copra-rolled oats (1:4), peanut butter-rolled oats (1:6), and corn oil-rolled oats (1:15) against oats as a standard. Interaction was not significantly greater than Error, but Baits were highly significantly greater than Error. Trial 19 compared copra-oats at

three concentrations (1:4, 1:6, 1:9) with oats. Interaction was not significant, but Baits were significant. In this trial the Baits were not significant within replicates. Trial 7 tested copra-rolled oats (1:4), copra cake-rolled oats (1:4) and copra oil-rolled oats (1:13.3) with oats as a standard. The two replications had almost the same overall acceptance. Interaction was less than Error and Baits were highly significant.

Other trial types were considered, but only one was tested. This method placed different pairs from four baits in stations, and the six stations were arranged in a circle 200 feet in diameter to allow visitation of any station at random. The six bait-pair combinations were rotated randomly among the stations for six days, but with the restriction that a pair occurred only once each day and once in each station. Apparently the rats did not like the constant change of baits because acceptance was very low despite the fairly heavy population density and highly acceptable baits. Such a test if successful in operation would give variances due to stations, days, pairs of baits, and baits, enabling the investigator to test bait differences and differential effects of paired baits.

SUMMARY

Bait acceptance trials for use with wild rats were developed during studies on the island of Guam to determine preferred baits for use in poisoning campaigns.

Feeder stations were constructed for conducting the trials.

Various baits were evaluated against a standard bait of plain rolled oats, using the criterion of significance of difference between mean acceptances. Rolled oats was repeatedly demonstrated to be the cereal of choice.

Three oily bases were superior as adjuvants to the cereal, in the following order; ground fresh copra, copra oil, and peanut butter. The optimum ratio of copra to rolled oats was found to be 1:4 to 1:6.

Replications of trials give important additional evidence. Significance of differences became more reliable as the degrees of freedom attributable to error increased. The validity of using interaction as the error term in single trials was substantiated by the analysis of replications.

BONE GROWTH AS AN AGE CRITERION IN THE COTTONTAIL RABBIT[1]

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This paper is a preliminary report on the progressive ossification of bones as an age criterion in the cottontail (*Sylvilagus floridanus mearnsi*). Ossification is expressed by the gradual disappearance of the epiphyseal cartilage and its

[1] Professor A. D. Hasler suggested the application of the X-ray method, Professor Aldo Leopold gave advice and a critical reading of the manuscript, and Robert McCabe furnished specimens, including the banded adult of known age.

replacement by bony material.

Our purpose is to develop a test by which cottontails shot in late autumn, or trapped in autumn and winter, may be classified into young and old, just as the bursa of Fabricius is now used to classify game birds. The essentials are that the test be:

1. Applicable to either live or dead specimens.
2. Valid through the hunting season (mainly November) and as far as possible into the trapping season (November to March).
3. Applicable to some bone which hunters are willing to spare and can send by mail from distant points.

OTHER AGE TESTS

Elder and Sowls (1942) have described a method of classifying cottontails for age by examining the testes and uteri in carcasses. Their test seems to be good into December but is, of course, not applicable to live rabbits. Dice and Dice (1940) worked out dentition tests for age, but these are applicable only to very young rabbits. Our hope is to develop a test which can be applied to live rabbits by X-ray of some standard bone, or to dead rabbits by either X-ray or gross staining of some standard bone.

MATERIALS AND TECHNIQUES

To determine how far into the winter the epiphyseal cartilage could be demonstrated, we examined the bones of a series of 52 cottontail rabbits collected through the autumn and winter of 1944–45. Each rabbit was examined first by X-ray, and later sample bones were cleaned and stained. The series included one rabbit (no. 163) bearing an ear tag of the previous winter; this individual was thus known to be an adult.

All of the rabbits were collected by shooting in the University of Wisconsin Arboretum. Forty-four were entire rabbits taken between October 3, 1944, and January 3, 1945. Legs of eight additional rabbits were obtained from hunters on January 28 and February 4, 1945. The rabbits were brought to the laboratory, where they were first weighed, tagged and sexed. An X-ray film of one foreleg was then made routinely, using the following technique: 50 MA., 36 KVP., 0.15 sec., distance 30 inches, Eastman ultraspeed film, detail screens. Films of the entire skeleton were made of 13 specimens to determine whether any other region was more suitable for study than the foreleg.

To compare the X-ray test with the staining test, the humerus of each specimen was removed for staining. It was first boiled for 10 minutes in dilute citric acid (2 grams per liter of water). The soft tissue was then readily removed. Donaldson and Conrow (1920) and Green (1934) have described methods of cleaning bone that also have been employed successfully. The method described by Green is particularly good for specimens stored in alcohol or formaldehyde.

After being cleaned, the bone was placed in a cartilage stain. If no quantitative studies or histological sections are to be made, immersion for 12 to 24 hours in an aqueous stain of 10 mg. acid fuchsin or 25 mg. nile blue per liter, would differentiate the epiphyseal cartilage from the adjacent bone. Should more detailed information be desired, the methods of Dawson (1926), Macklin (1917), Richter (1937), or Richmond (1938) are suggested.

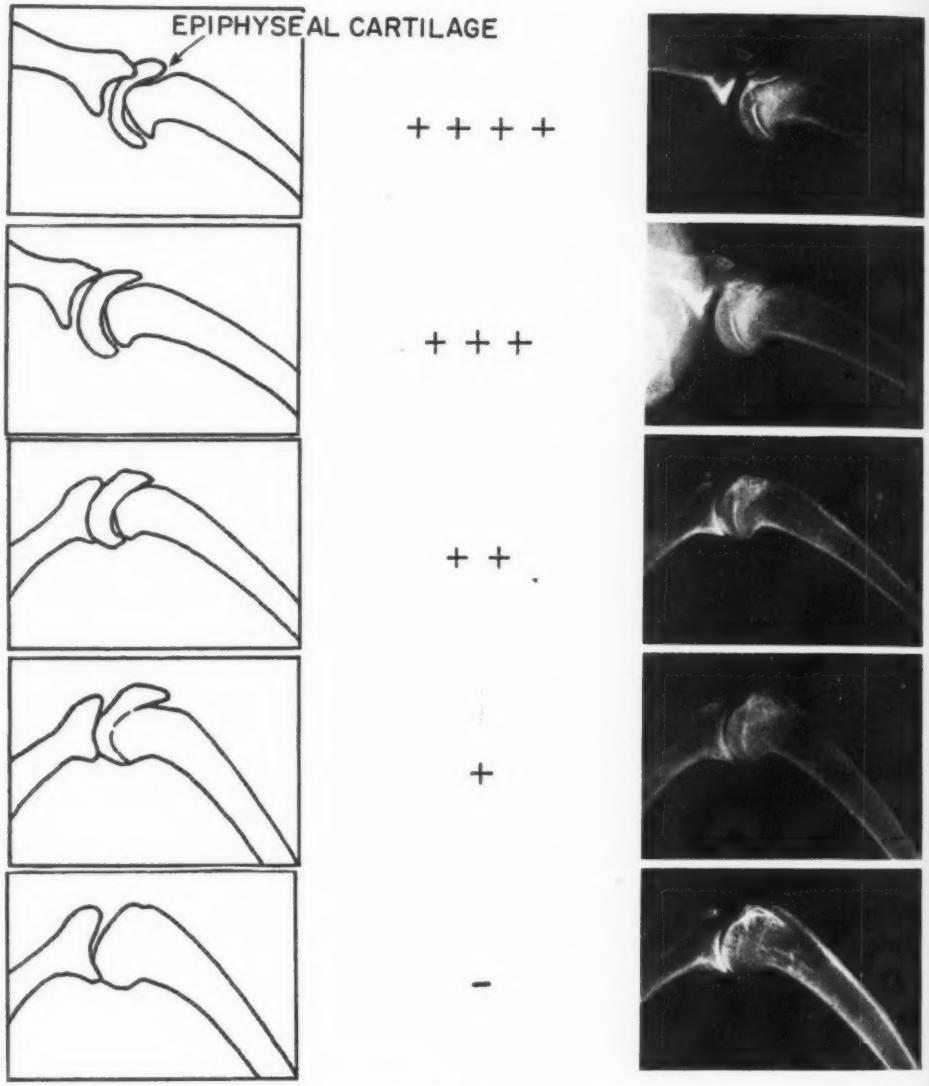
Table 1 records the data obtained from X-ray films of the forelimbs. The

TABLE 1.—RELATIVE AMOUNT OF EPIPHYSEAL CARTILAGE IN THE SHOULDER AND ELBOW REGIONS OF 52 COTTONTAIL RABBITS X-RAYED OCTOBER 1944 TO JANUARY 1945

++++, full cartilage; −, no visible cartilage

Date collected	*No.*	*Sex*	*Weight, grams*	*Relative thickness of epiphyseal cartilage*	
				Shoulder (humerus)	*Elbow (ulna)*
10- 3-44	1	Female	1350	+++	+++
10- 5-44	2	Female	850	++++	++++
10- 5-44	3	Male	1206	+++	+
10-10-44	4	Female	671	++++	++++
10-10-44	5	Male	1174	++++	+
10-21-44	6	Female	1194	++	−
11- 3-44	7	Male	721		
11- 3-44	8	Male	1010	++++	++++
11- 9-44	9	Female	1579	−	−
11- 9-44	10	Male	1286	+++	+
11- 9-44	11	Male	1094	++++	++++
11-12-44	12	Male	685	++++	++++
11-12-44	13	Female	910	++++	++++
11-12-44	14	Male	1224	++	+
11-16-44	15	Male	1164	++	−
11-19-44	16	Female	1237	++	−
11-30-44	17	Male	1247	+	++
11-30-44	18	Female	1151	++	+
11-30-44	19	Female	1265	+	−
11-30-44	20	Male	1301	+	−
12- 5-44	21	Male	1320	+	−
12- 5-44	22	Male	1225	+	−
12- 6-44	23	Female	1312	+	−
12- 7-44	24	Female	1377	−	−
12-17-44	163[a]	Male	1207	−	−
12-20-44	25	Male	1312	+	−
12-20-44	26	Female	1068	+	−
12-20-44	27	Male	918	+++	−
12-20-44	28	Male	1115	+	−
12-20-44	29	Female	1347	−	−
12-20-44	30	Female	1040	++	−
12-20-44	31	Female	1252	+	−
12-21-44	32	Female	1241	+	−
12-28-44	33	Male	1249	+	−
12-28-44	34	Male	1062	+	−
12-28-44	35	Male	1157	−	−
12-28-44	36	Female	1022	++	−
12-28-44	37	Male	1177	++	−
12-28-44	38	Female	1274	++	−
12-28-44	39	Female	1436	+	−
1- 3-45	40	Female	1214	++	−
1- 3-45	41	Female	1007	+	−
1- 3-45	42	Male	1197	−	−
1- 3-45	43	Female	1242	+	−
1-28-45	44a	Not sexed	Not weighed	−	−
1-28-45	44b	Not sexed	Not weighed	−	−
1-28-45	44c	Not sexed	Not weighed	−	−
1-28-45	44d	Not sexed	Not weighed	−	−
1-28-45	44e	Not sexed	Not weighed	−	−
2- 4-45	45a	Not sexed	Not weighed	−	−
2- 4-45	45b	Not sexed	Not weighed	+	−
2- 4-45	45c	Not sexed	Not weighed	−	−

[a] An ear-tagged individual recaptured from previous winter, and thus known to be adult.



X-ray photographs (right) and interpretive drawings (left) showing gradual disappearance of epiphyseal cartilage in the shoulder region, corresponding to the four categories used to classify cottontail rabbits as to age in Table 1.

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relative amount of epiphyseal cartilage present at the shoulder and elbow regions was estimated and is indicated by plus (+) marks. Plate 14 shows the four stages of decrease in cartilage at the shoulder corresponding to four, three, two and one plus marks, and also the final stage of complete ossification (−); the illustrations are from rabbits nos. 11, 10, 36, 26, and 24. Rabbit no. 163, an adult, exhibited the complete ossification of stage 5 in plate 14, but was not shown because the photograph happened to be inferior.

It is evident (Table 1) that the epiphyseal cartilage persists longer at the shoulder than at the elbow, and that the shoulder region, therefore, can be used as a criterion of age over a longer period than the elbow region. Study of the complete series of skeletal X-rays of 13 specimens indicated that in the knee region, especially at the upper end of the tibia, the epiphyseal cartilage persists at least as long as at the shoulder. The cartilage at the upper end of the tibia offers another slight technical advantage referred to later. Since hunters are more likely to contribute forelegs than hindquarters, however, the forelimb is here proposed as the standard bone for the study of rabbits from hunters' bags.

LIMITING DATES

A population can be classified for age with accuracy as to individuals only up do the date on which the epiphyses close in the earliest-born young. To determine this date, a series of rabbits of known age are needed. To this end, Robert A. McCabe and James B. Hale trapped and ear-tagged a series of young cottontails in summer, for subsequent recapture during the winter; 70 young were tagged during the summer of 1945, but the rate of recapture will be low and several years may be required to establish the limiting dates for the various epiphyses. Meanwhile we are publishing at this preliminary stage, because our work was interrupted by military duty in February 1945.

Table 1 gives a preliminary notion of what the limiting dates may be. Some rabbits retained open epiphyses at the shoulder until early January, and at the elbow until late November. Those individuals presumably were late-born young. How much earlier the epiphyses of the early-born young would close will remain a matter of conjecture until a series of marked young is recaptured. At a guess, the shoulder should be a safe criterion through November, during which month most rabbits are taken by hunters.

Changes in the architecture of the skeleton do not cease abruptly with the replacement of the epiphyseal cartilage by bone. Reorganization of the pattern of the bony trabeculae continues for some time after fusion, and such change also can be used to classify for age. No attempt was made in this study, however, to collect suitable material, or to extend interpretation beyond the stage of fusion.

X-RAY VS. STAINING

In several rabbits, the gross staining procedure showed the presence of cartilage despite negative results by the X-ray method. This is because the epiphyseal cartilage is not a flat plate, but is irregularly cone-shaped. There is, therefore, an overlapping of bone and cartilage recorded on the film by the X-rays. Such films are difficult to read accurately when only a small amount of

cartilage is present. The cartilage at the upper end of the tibia, however, approaches a flat plate, and less disagreement would be expected between X-ray and staining in this joint than elsewhere.

The 44 entire rabbits collected up to January 3 are inadequate as a sample of the population, but the sexes were equally represented in the two age groups:

	Males	*Females*	*Totals*
With epiphyses, known to be young	19	19	38
Without epiphyses, adult, plus perhaps a few early-born young	3	3	6
	22	22	44

Young rabbits constituted at least 86 per cent of the sample. Since some early-born young may have displayed closed epiphyses by January 3, the actual percentage of young possibly was greater.

The weights suggest that females average heavier than males and that the heaviest young weigh more than the lightest adults. All of these indications conform to the findings of Elder and Sowls.

The flushing rate during 50 hours of hunting was 1.9 rabbits per hour, which is somewhat higher than the 1.6 recorded by McCabe (1943) for all of Wisconsin in 1940.

SUMMARY

1. Young-of-the-year can be differentiated from adult cottontails by X-ray of the bones or by staining the bones to show the presence or absence of epiphyseal cartilage.

2. This cartilage persists in the shoulder regions of some young rabbits (presumably the latest-born young) until January, and probably persists in the earliest-born young through November, during which month most rabbits are taken by hunters. Further verification is needed of the safe terminal date for age-classification by various bones.

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BRIEFER ARTICLES

A COMBINATION PHOTOELECTRIC LIGHT METER AND FISH-DETECTOR[1]

A combination light meter and photoelectric fish-detector (ichthyometer) has been used with success to chart migration times of perch in Lake Mendota, Madison, Wisconsin. This method facilitates the study of schooling species of fish where the transparency of the water and adverse light conditions preclude direct visual observation. The advantages over other indirect methods such as use of nets are obvious.

Since the summer of 1943 we have been charting the movements of perch schools over a "bank" just off Second Point on Lake Mendota. These migrations took place at or near sundown. To refine the correlation between migration and light, it was desirable to measure the intensity of light reaching the levels where the perch feed.

The junior author was assigned to devise an instrument that would measure very small quantities of light reaching 3 to 4 meters below the water surface at sundown. He learned that an apparatus (Fig. 1) previously used to study microstratification of inland lake waters (Whitney, Wisconsin Acad. Sci. Trans., 31: 155–173, 1938) would detect the presence of swimming fish. The latter obstructed the beam of light producing the deflections ("kicks") of the microammeter. The photocell was arranged to be directed upward for daylight intensity measurements or horizontally toward the light source. The mechanism for rotating the cell was controlled by a cord reaching to the surface. When the photocell was faced toward the light source, the apparatus operated as a fish detector, sudden deflections were plainly observed on the microammeter as fish interrupted the beam. The intensity of the light source was kept low (6-volt bulb) so as not to attract or repel the fish any more than could be avoided. The light, moreover, was turned out periodically so as not to furnish a continuing attraction for the fish. The distance between photocell and light source was made as large as conveniently possible for use in a row boat 4 ft. wide. At first it was thought that it would be necessary to provide wing nets to direct the fish into the beam but this proved unnecessary.

A satisfactory correlation was found between the deflections per minute and the number of fish caught either in gill nets over definite periods or by hand lines from the same or nearby boats.

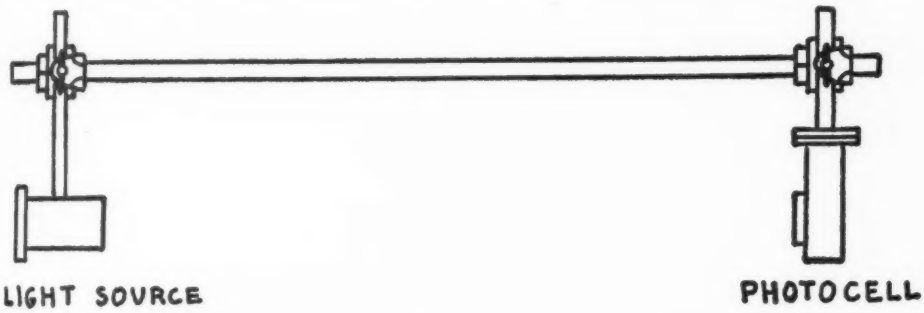

Fig. 1. Photoelectric fish detector. (Rotating device for photocell not shown.)

A two-stage photocell amplifier was used in the initial measurements, the first stage being in the underwater housing. Maximum sensitivity was desired to measure daylight intensities in 3–4 meters of water both before and after sundown. Intensities as low as 0.01 foot candle were detected. A revision of this equipment, involving reduction in physical size, is in progress.

[1] Supported in part by a grant from the Wisconsin Alumni Research Foundation.

Another fish-detector has been constructed with a single stage amplifier having enough sensitivity for fish detection. This equipment is small both in physical size and weight. Controls are mounted on a panel 7×8 inches and the box is about 7 inches deep. Only two batteries, a 1.5-volt A battery and a 90-volt B battery are needed (Fig. 2). The 3Q5 tubes use only 0.1 ampere for filament current at plate current with its resultant degenerative effect on the grid bias of tube no. 1. Stability was further improved by grounding the positive lead of the photocell to the underwater case, and grounding the panel to the B^+ lead.

In operating the amplifier, the microammeter is brought to a zero reading under conditions of no light by means of the adjustment R_1 and the fine adjustment R_4. A

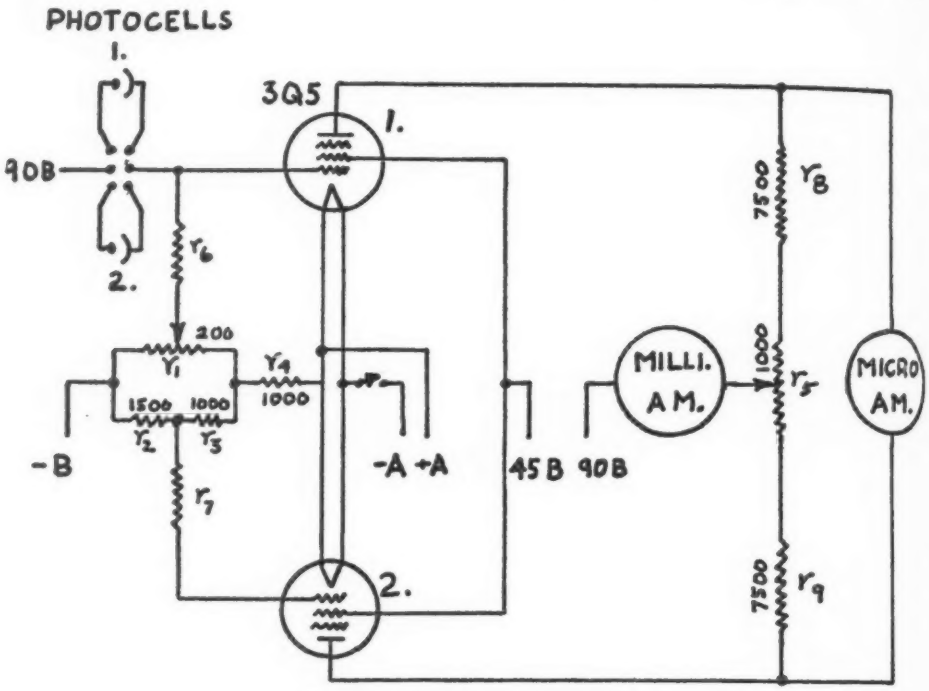

Fig. 2. Photocell amplifier circuit.

1.5 volts, and have a relatively high mutual conductance. The necessary grid bias for the tubes is obtained by the potential drop of the plate current through the resistors R_1, R_2, R_3, and R_4. The photocell current affects only the grid of tube no. 1. A circuit of the push-pull type was tried with a separate photocell battery, but unstable conditions resulted unless extreme care was taken to insulate the case of this battery. This battery and its case were at the potential of the grid of tube no. 2. The advantage in omitting this battery more than counterbalances the slight loss in sensitivity owing to the variable total

double throw switch makes it possible to connect the amplifier to either of two photocells. Readings may be taken with two fish-detector units under water at different depths, or with one detector unit under water in addition to a photocell above water for recording daylight intensities. In this way, the presence or absence of correlation between daylight intensities and fish movements may be verified.

Initial results show that the detector differentiates between small, medium, and large schools of perch, and therefore has a variety of applications such as observing: (1) activity and movements at night, (2) at depths be-

yond the range of vision, (3) in turbid waters, and (4) in winter under the ice.—ARTHUR D. HASLER and LESTER V. WHITNEY, *Department of Zoology, University of Wisconsin, Madison, Wisconsin, and Department of Physics, Southwest Missouri State Teachers College, Springfield, Missouri.*

CALCULATING POISON BAIT MIXTURES

There is wide range in the proportions of bait, poison, and other ingredients in the different mixtures employed for the control of various species of harmful rodents. Some even include unlike measures of quantity, such as ounces of strychnine and quarts of barley in the standard "government" formula for ground squirrel control. Whenever a quantity of any bait is to be prepared, some calculations are necessary unless the amount desired is exactly that of an available formula. If the quantity is some fraction or multiple, the weight of each ingredient must be figured. More elaborate calculations are necessary if it is desired to change an existing formula or to compare two or more formulas.

Much time may be saved in these and similar problems by the use of a nomogram with which, knowing the values for any two items, the third may be quickly ascertained. The accompanying chart (Fig. 1) has been prepared to facilitate the calculation of poison mixtures for rodents. *A straight line through any two known values will mark that of the third item.* Users should note that all of the scales are logarithmic (to afford a wider range of values within limited space), and this should be kept in mind when interpolating values between those marked or numbered on the scales.

For example, the chart will immediately show that 10 pounds of bait with 1 per cent of poison requires 1.6 ounces (45 grams) of the latter; or a 1 per cent mix using 1.6 ounces requires 10 pounds of bait; or 10 pounds of bait and 1.6 ounces of poison yields a 1 per cent mix.

For use with any cereal bait measured in quarts, the value for bulk measure must first be projected horizontally to the "bait-pounds" scale; it then is easy to determine the percentage of poison when using a specified weight of the latter, or vice versa. Thus 16 quarts of whole barley weigh about 23 pounds; and this amount with 1 ounce of strychnine makes a mixture with 0.26 per cent poison. With oats, however, 16 quarts weigh only 16 pounds and when used with 1 ounce of poison the mix is 0.39 per cent or 1:250.

By simple decimal changes, values other than those shown directly on the chart may be determined. If, for example, 16 pounds of a 0.26 per cent mix of poison with oats is required, the value for the poison cannot be read directly on the scale; however, a line from 16 pounds on the bait scale through the 2.6 per cent point (10 times the required poison value) on the middle scale will mark 7 ounces (10 times the required value) on the poison scale; hence, 0.7 ounces of poison is the correct value with 16 pounds of bait for a 0.26 per cent mix. Again, for 1,000 pounds (1/2 ton) of bait in a 0.26 per cent mix, a line from 100 pounds (1/10 of the required value) on the bait scale through 0.26 per cent shows that 4.2 ounces of poison is 1/10 of the total amount needed (42 ounces) of the latter.

For bait formulas stated in odd amounts and proportions of poison the chart provides means to convert to suitable values for comparison with other preparations. For example, one formula prescribes ground bread crumbs, 35 parts; peanut butter, 5 parts; and molasses, 5 parts. This is to be used with zinc phosphide at 1:160 for mouse control. A line through the total weight of bait (45 pounds) and the ratio (1:160 or 0.625%) shows 4.35 ounces as the correct amount of zinc phosphide to employ. If it were desired to make up only 10 pounds of such mixture, a line from 10 pounds through the ratio point (1:160) would indicate just over 1 ounce as the requisite amount of poison needed.

Calculations that involve mixtures with large proportions of poison such as barium carbonate (20% mix) or red squill (10% mix), will show the total weight of bait plus poison

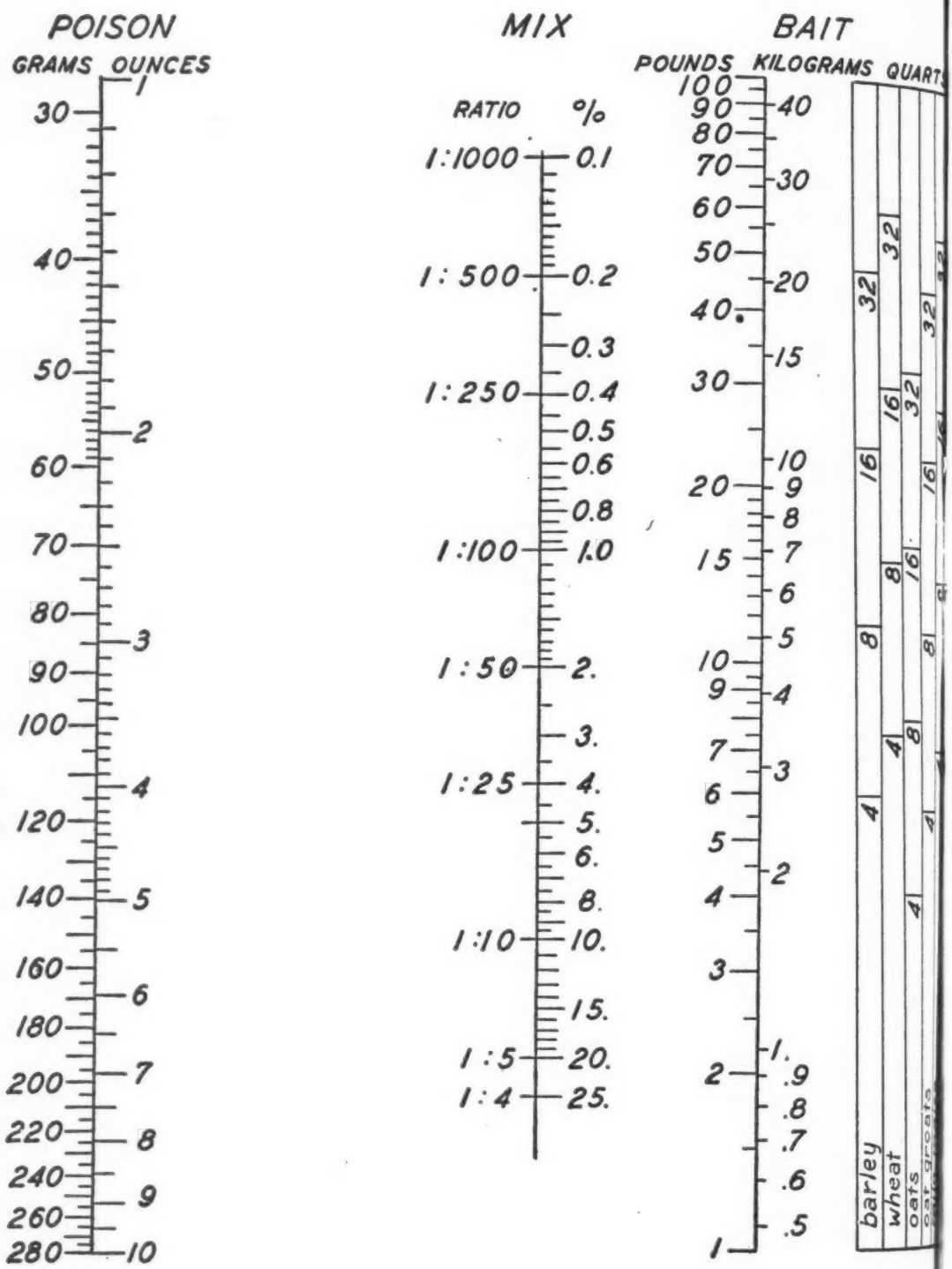

Fig. 1. Nomogram or alignment chart for calculating poison bait mixtures.

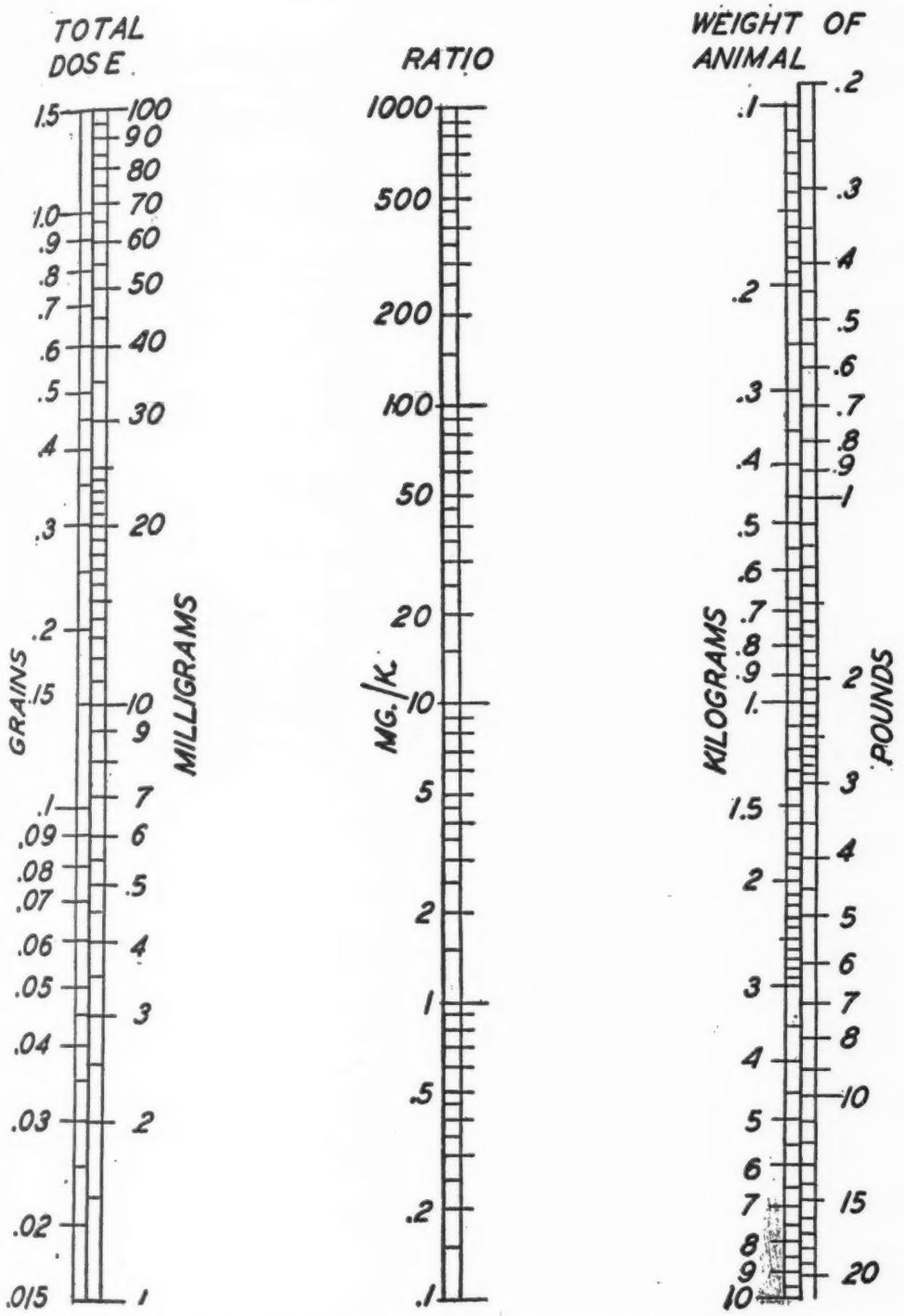

Fig. 2. Alignment chart for calculating dosage in relation to weight of animal.

on the right hand scale. Thus, with 10 ounces of red squill in 10 per cent mix, the total weight of the mixture is 6.3 pounds, of which 5.7 pounds is bait.

The conversion figures for cereals from bulk measure to weight are based on values in the "Handbook of official grain standards of the United States" (U.S.G.S.A. no. 90, revised October 1940; published by Agricultural Marketing Service, U. S. Department of Agriculture). Values therein per U. S. Standard Bushel (32 quarts), No. 1 grades, in pounds, are as follows: wheat, 60; corn (and rye), 54; barley, 47; milo maize, 55; oats, 32. An approximate value for oat groats (kernel less outer coat) is 44.5 pounds per bushel.

These weight values for cereals have been used on the chart, although the exact weight per bushel of any particular cereal will vary with locality, variety, and manner of threshing. Sacked grain will likewise vary somewhat in weight and number of bushels per sack: wheat, 125 to 140 pounds, barley 100 to 120 pounds, etc. If precise values are needed, the operator should determine the weight to bulk ratio of his local supply and make the necessary corrections on the scales at the right of the chart. In like manner, the weight-to-bulk ratio of any other bait material may be added to the chart for convenience in preparing mixtures.

Often it is convenient to weigh poison in grams and bait in pounds; for this purpose metric equivalents are shown on the left side of the poison scale of the chart. For conversion of scale value (avoirdupois) to metric equivalents, 1 ounce = 28.35 grams and 1 pound = 0.453 kilogram. It should be remembered that the apothecary or troy ounce is of 480 grains (= 31.103 grams), whereas the avoirdupois ounce used here is of 437.5 grains (= 28.35 grams).

The second nomogram (Fig. 2) is useful in experimental studies with poisons. Both metric and avoirdupois values are available for the dose and for the weight of the animal. When any two values are known, a straight line through these will intersect the third (unknown) value. As an example, when using a poison with toxicity of 25 milligrams per kilogram (of animal weight), and considering a ground squirrel weighing 0.6 kilogram (1.3 pounds), this nomogram will show that the animal must eat enough bait to carry 15 milligrams (0.225 grain) of poison for a fatal dose. By determining (from Fig. 1) the percentage mix in any poison bait formula, it then is possible to ascertain the toxic dose of that poison mix for an animal for which the toxicity of the poison and body weight are known.—TRACY I. STORER, *Division of Zoology, University of California, Davis, California.*